Modelling the spatial dispersal of aquatic invertebrates to predict (re-)colonisation processes within river catchments

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Dedicated to my new-born son, Henri

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Abbreviations

CCR Correct classification rate

CON Conservative dispersal modelling approach

DGM Digital elevation model

FN False negative prediction (here: species observed, but not predicted by dispersal models to be present)

FP False positive prediction (here: species not observed, but predicted by dispersal models to be present)

GIS Geographic information system

LC Least-cost dispersal modelling approach

SU Spatial unit

TN True negative prediction (here: species not observed and not predicted by dispersal models to be present)

TP True positive prediction (here: species observed and predicted by dispersal models to be present)

TSS True skill statistic

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1. Introduction

1.1. Motivation to study dispersal

Aquatic resources and ecosystems have been degraded for decades and continue to be degraded due to various human water uses and ecosystem modifications. In Europe, extensive water quality deterioration dates back to the 1960s when industrial and urban development increased rapidly. The industrialisation era came along with excessive wastewater and contaminant loads that caused severe deterioration of aquatic life and biodiversity. Combined with water quality deterioration, aquatic habitats have been physically degraded. For example, streams and rivers have been straightened, enforced, regulated, and dammed to support agricultural, industrial and municipal water uses. This structural degradation has put additional threats on aquatic life. Consequently, wastewater treatment was implemented in the 1970s to reduce organic and contaminant loads and enhance water quality. Later, hydrological and morphological restoration began with the intent to restore ecosystem functionality and enhance habitat diversity.

Since the year 2000 these efforts are supported by the European Water Framework Directive (Directive 2000/60/EC) with the objective to achieve a good ecological status for rivers and stream across Europe, assessed by status of riverine biota, represented by aquatic invertebrates, aquatic flora and fish fauna. However, although substantial investments have been made in restoration (e.g., Bernhardt et al. 2005, Bernhardt et al. 2007), biological recovery after restoration often does not reflect these investments or the associated efforts (e.g., Feld et al. 2011, Haase et al. 2013, Palmer et al. 2010). The list of explanations for the failure of ecological recovery is long: restoration is not effective (e.g., too small to sustain pristine habitat characteristics), stressors continue to impact restored sites and hence hamper recovery (e.g., excessive agriculture in the catchment above; significant legal industrial wastewater influents), or previous degradation was too widespread leading to a regional extinction or fragmentation of source populations required for recolonisation, just to name a few reasons. Therefore, dispersal is the central ecological mechanism that determines colonisation and of rivers in a

fragmented riverscape. Connectivity between source populations and restored sites can be limited by dispersal barriers and was found to be important to explain recolonisation patterns (Winking et al. 2014).

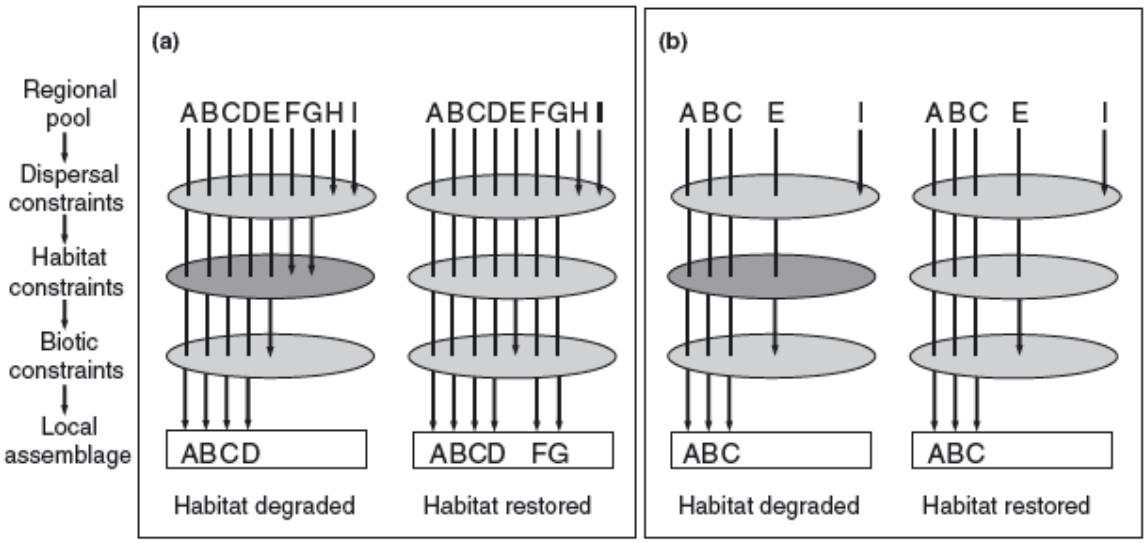

Figure 1: (reprinted from Lake et al. 2007) Hypothetical outcomes of habitat restoration on a local species assemblage with (a) intact and (b) depleted regional species pools. Restoring habitat when the regional species pool is intact allows species F and G to pass through the environment-constraint filter and thus contribute to the local assemblage. However, when the species pool is depleted, comprising only resistant species, restoring habitat does not result in species additions at the local scale (adapted from Rahel 2002).

The presence of nearby source populations (regional pool) and the absence of dispersal constraints is a requisite for ecologically successful restoration in theory (Lake et al. 2007), as described with Figure 1 (a) versus Figure 1 (b). But, although dispersal is widely acknowledged as the central mechanism for recolonisation, there are only a few studies in restoration ecology. Therefore, this thesis will focus on the dispersal of aquatic invertebrates as a requisite for the (re-)colonisation of rivers.

1.2. Scope of thesis

The following main chapters cover different ecoregions (Figure 2) with a lower mountainous catchment (Chapter 2) and lowland catchment (Chapter 3) and different model species in terms of dispersal capabilities, including the aquatic

insect orders Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera and Odonata (hereafter also referred to as aquatic insects or benthic invertebrates). Both main chapters were prepared separately for publication purposes. Chapter 2 was published in an international peer-reviewed journal (Sondermann et al. 2015). Chapter 3 is actually in print in an international peer-reviewed journal (Sondermann et al. in print).

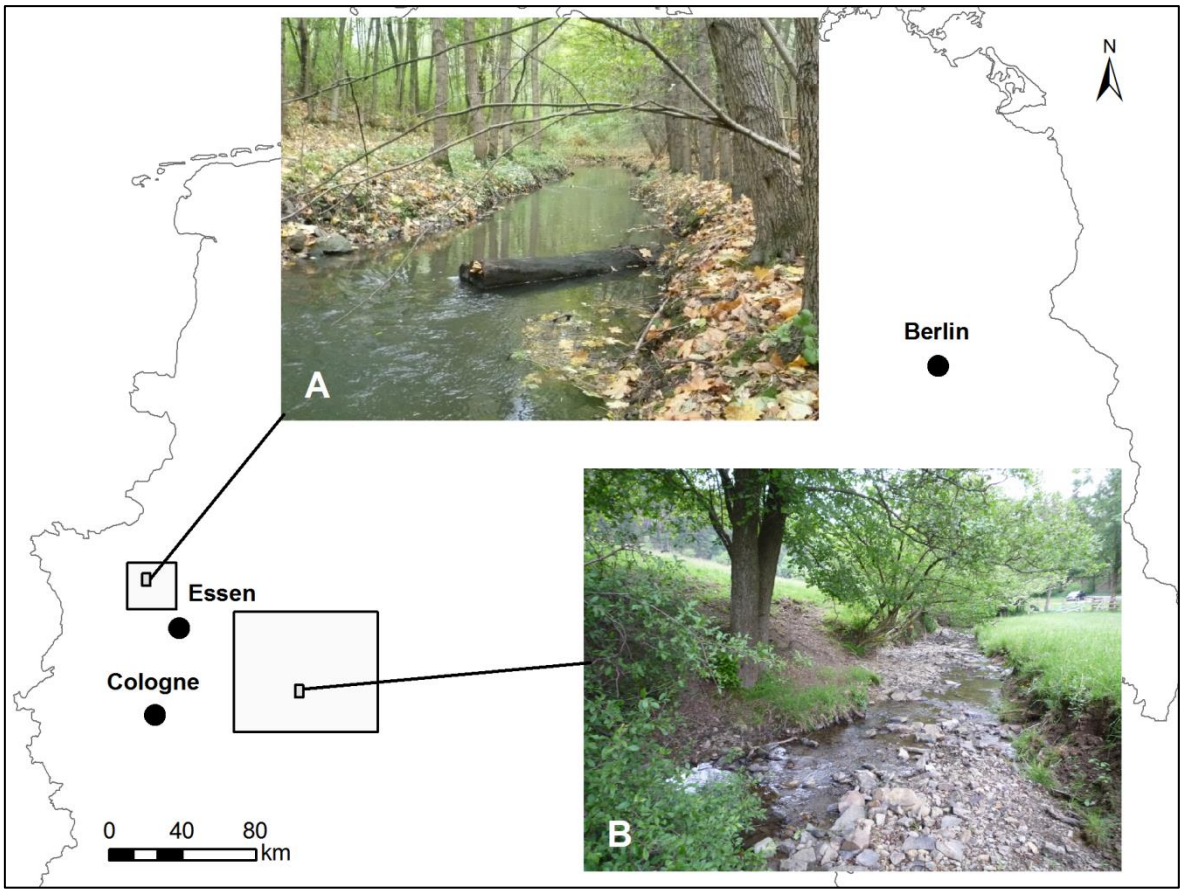

Figure 2: Study area for the present thesis covers two different ecoregions with the Boye system in the lowland (e.g., Picture A: Boye near Ellinghorst) and Ruhr system in the low mountain range of Germany (e.g., Picture B: Settmecke near Stockum).

Chapter 2: Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment

Strong dispersers play an important role as pioneers, recolonising faster than weak dispersers (Li et al. 2016). One can contrast this exemplarily with physiologically high performance dragonflies with clumsily flying stoneflies or short

living mayflies. But, e.g., long distance movements have been found in taxa beyond Odonata, often wind-assisted, as shown in Johnson (1969). To explore dispersal of aquatic insects with regard to the recolonisation of rivers, it was fundamentally to screen the actual knowledge in literature for details on dispersal capacities and possible dispersal distances. To contribute to a better understanding of dispersal, the results of this literature survey should be aggregated in spatially explicit dispersal models to make predictions on potential dispersal ranges of benthic invertebrates and to evaluate the effect of physical dispersal barriers.

Therefore, chapter 2 focusses on two main objectives:

- The survey on the recent knowledge on dispersal distances and dispersal barriers of aquatic insects in literature.
- The development of spatially explicit dispersal models, considering taxon-specific dispersal distances and barriers.

Chapter 3: Application and validation of a new approach for modelling benthic invertebrate dispersal: first colonisation of a former open sewer system

In a former study, assemblages of aquatic fauna communities and surrounding source populations were found to be highly correlated within a distance of 5 km (benthic invertebrates: Sundermann et al. 2011a; fish fauna: Stoll et al. 2013). Following this finding, we contrasted a dispersal modeling approach, based on this rule of thumb (5 km) with a “least-cost” modeling approach that considers species-specific dispersal distances and dispersal barriers. The dispersal models were developed for a study area (river Boye) which is part of the Emscher system in North-Rhine Westphalia, Germany. The Emscher System gained a certain degree of prominence as one of the last open sewer systems; the downstream third of the river network still serves as such and almost exclusively conveys untreated domestic wastewater. The Boye system is located in the middle third of the catchment and upstream parts of the former open sewer system have been revitalised since 1993 (Winking et al. 2016). Since then most tributaries of the Boye system are free of sewage. Single tributaries of the Boye system and adjacent streams never conveyed sewage and thus constitute refugia for benthic

invertebrates. After revitalisation, these refugia served as origins for recolonisation and hosted the source populations. The combination of the known distribution of refugia, together with the knowledge of the parts of the Boye system that were free of benthic invertebrates before revitalisation opened an unprecedented option to study the recolonisation of the system. Any species found at a formerly polluted site must have recolonised the site starting from one of the known refugia.

In particular, the latter point motivated us to study the potential recolonisation by modelling the dispersal of aquatic organisms, namely the presence and absence of 18 benthic invertebrate taxa in more than 35,000 spatial units. This approach uses actual presences and absences and thus is prone to false negatives (i.e., species might have been overlooked during sampling). Fortunately, the characteristics of our model catchment allowed us to reduce this uncertainty. Prior to its restoration a few years ago, the restored sites were open sewers that transported untreated wastewater. Thus, we anticipated that none of the targeted habitat sensitive model taxa inhabited the sites (Winking et al. 2016). Consequently, the recolonisation of the site after restoration is likely to originate from a source population within the model catchment. It is this peculiarity of the Boye system that allowed us to develop the least-cost dispersal models and to compare our results with those of a purely distance-based (conservative) approach following the findings of Sundermann et al. (2011a) and Stoll et al. (2013).

Therefore, chapter 3 focusses on the following objective:

- The validation and comparison of a dispersal modelling approach, based on taxon-specific dispersal distances and barriers, against a purely distance-based approach.

2. Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment

2.1. Introduction

Lotic aquatic insects are often patchily distributed within catchments, because their life-cycle-specific habitat requirements are not evenly fulfilled throughout the whole catchment. Eggs, larvae, pupae and adults have different ecological demands (Rosenberg & Resh 1993), including bottom habitats, water chemistry, temperature and riparian vegetation. Consequently, most species prefer those river zones, that best correspond to their ecological requirements, e.g., concerning temperature and flow velocity (Hussain & Pandit 2012).

Anthropogenic habitat alterations due to river modifications (e.g., stagnant zones near dams) fundamentally alter benthic assemblages. Pollution may eradicate local populations entirely, or at least decrease their abundance. As a consequence, suitable habitat conditions are much more patchily distributed in altered systems than under natural conditions. Furthermore, contemporary distribution patterns may be impacted by legacy pollution (Harding et al. 1998) that mostly decreased decades ago but that historically severely depleted populations in subcatchments. These populations continue to be impacted and require a long time to fully recover if recovery is feasible at all (Feld et al. 2011). The contemporary distribution patterns of lotic insects are therefore a combined result of natural habitat filters and present and past human alterations.

The exchange of individuals between sub-populations is controlled by dispersal, which is a fundamental prerequisite for sustaining biological diversity. There is also evidence that dispersal capacity is an important factor for the species ability to track environmental changes, e.g., global climate change (Hof et al. 2012). The main dispersal modes of aquatic insects are drift (downstream, active or passive), movement of aquatic larvae (up- or downstream, active) and aerial dispersal of

adult winged stages (active, passive), all of which primarily follow the stream corridor. Aerial dispersal can be directed lateral to the stream as well, i.e., independent from flow direction. Lateral dispersal can act across watershed borders so that individuals can disperse from one watershed to another (Hughes 2007, Macneale et al. 2005). Dispersal distances and capabilities, however, are also affected by barriers (Bohonak & Jenkins 2003, Lake et al. 2007, Parkyn & Smith 2011). Weirs and dams often inhibit upstream dispersal, and stagnant zones can act as sinks for drifting lotic species (Vinikour 1980, Vinikour 1981). Winged adults, such as damselflies, stoneflies and caddisflies, often prefer specific microclimatic and light conditions for dispersal and may stop dispersing if conditions change, e.g., due to shade and lower temperatures close to dense coniferous forests (Briers et al. 2002, Collier & Smith 1998, Hering 1992) or near settlements on the floodplain.

Dispersal distances and species-specific capabilities are important factors controlling an ecologically successful river restoration. There is increasing evidence that morphological restoration measures (e.g., remeandering or rebraiding of rivers, habitat enhancement) often do not result in significant changes in the benthic assemblage, despite strong and positive effects on the availability and quality of benthic habitats (Feld et al. 2011, Jähnig et al. 2009, Palmer et al. 2010). Besides ongoing habitat constraints (Brederveld et al. 2011), the most commonly assumed reasons for poor effects of river restoration on benthic invertebrates is the lack of re-colonisation potential, i.e., the lack of source populations capable of re-colonising a restored section (Feld et al. 2011, Sundermann et al. 2011b). This particularly refers to restorations in intensively used or heavily populated catchments, where self-sustaining source populations of many sensitive species have vanished almost completely. For example, Sundermann et al. (2011a) analysed 24 restoration projects and tested whether improvement of benthic invertebrate community depends on the presence of nearby source populations. They concluded that source populations within a radius of 5 km are significant predictors of biotic improvement.

Although the distance of 5 km for a successful recolonisation of restored stretches is a useful rule of thumb, actual recolonisation of restored sites may prove to be much more complex. Dispersal capabilities, dispersal mechanisms, reachable

distances and the barrier effects of aquatic and terrestrial structures largely differ among species. Furthermore, the current distributions of species differ and are often unknown at the scale of an entire catchment. This imposes limitations on the ability to make predictions based on generalisations.

In this study, we model the dispersal of three merolimnic insect species at the scale of an entire catchment – *Calopteryx virgo* (Odonata), *Dinocras cephalotes* (Plecoptera) and *Hydropsyche dinarica* (Trichoptera) – using a "least-cost" approach that has previously been used for terrestrial vertebrates (Adriaensen et al. 2003, Driezen et al. 2007), terrestrial invertebrates (Koch & Smith 2008), pollen dispersal (Trénel et al. 2008) and gene flow (Cushman et al. 2006, Spear et al. 2010), but rarely for aquatic organisms (Dedecker et al. 2007, Keller & Holderegger 2013). In particular, we aim to predict the species' potential dispersal based on (1) their present distribution patterns, (2) their life stages' dispersal capacities as documented in the literature or estimated by expert knowledge and (3) the potential barrier effects of different in-stream and terrestrial landscape structures. We used data on the presence and absence of the model species at nearly 1,200 sampling sites within the catchment, which can be expected to form a reliable basis for modelling species' possible dispersal range from known source populations and helps to overcome the limitations to dispersal modelling as outlined above.

In particular, we addressed the following questions:

- Which river sections within the catchment are accessible for the model species?
- How do different dispersal mechanisms (aquatic upstream, aquatic downstream and aerial dispersal) contribute to the accessibility of the catchment by merolimnic species?
- How do in-stream and terrestrial landscape barriers impact dispersal patterns?

2.2. Materials and methods

2.2.1. Study area and data source

The upper Ruhr catchment drains an area of 3,500 km^2 and is located in the Federal State of North Rhine-Westphalia, Germany (Figure 1). Altitudes within the predominantly mountainous catchment range from 100 to 730 m (a.s.l.). The floodplains of upstream reaches are primarily covered by coniferous forest, whereas agricultural, residential and industrial land use occur in most downstream sections. Many streams are disrupted by small dams and weirs, inducing lentic conditions upstream and lowered residual flows downstream of the weirs.

Benthic invertebrate taxa lists were available for 1,198 sites within the model catchment, of which 973 samples originate from regional surveillance monitoring and research projects (Dangel (personal communication), Frenz & Hering 2000, LANUV NRW (unpublished data), Maue 2006, Podraza et al. 2005, Rudolph 2011, Ruhrverband (unpublished data)). Monitoring data were obtained using “Multi-Habitat-Sampling” (Hering et al. 2004), which takes into account all present microhabitat types, by distributing 20 subsamples among these microhabitat types, according to their coverage. All microhabitats with an area of at least 5% of the whole sample stretch are considered. These data were complemented by additional field sampling in 2010 at 121 sites and 2011 at 104 sites (compare Gies et al. 2015a). Different from the monitoring samples mentioned above, this additional dataset was obtained by a time-based sampling methodology. Therefore, each site was sampled up to 100 m in length and for 45 minutes, in order to thoroughly scan all habitats relevant for the targeted model species. Thus, we aimed to reduce the chance of false negative records, i.e., a recorded absence when a species was actually present.

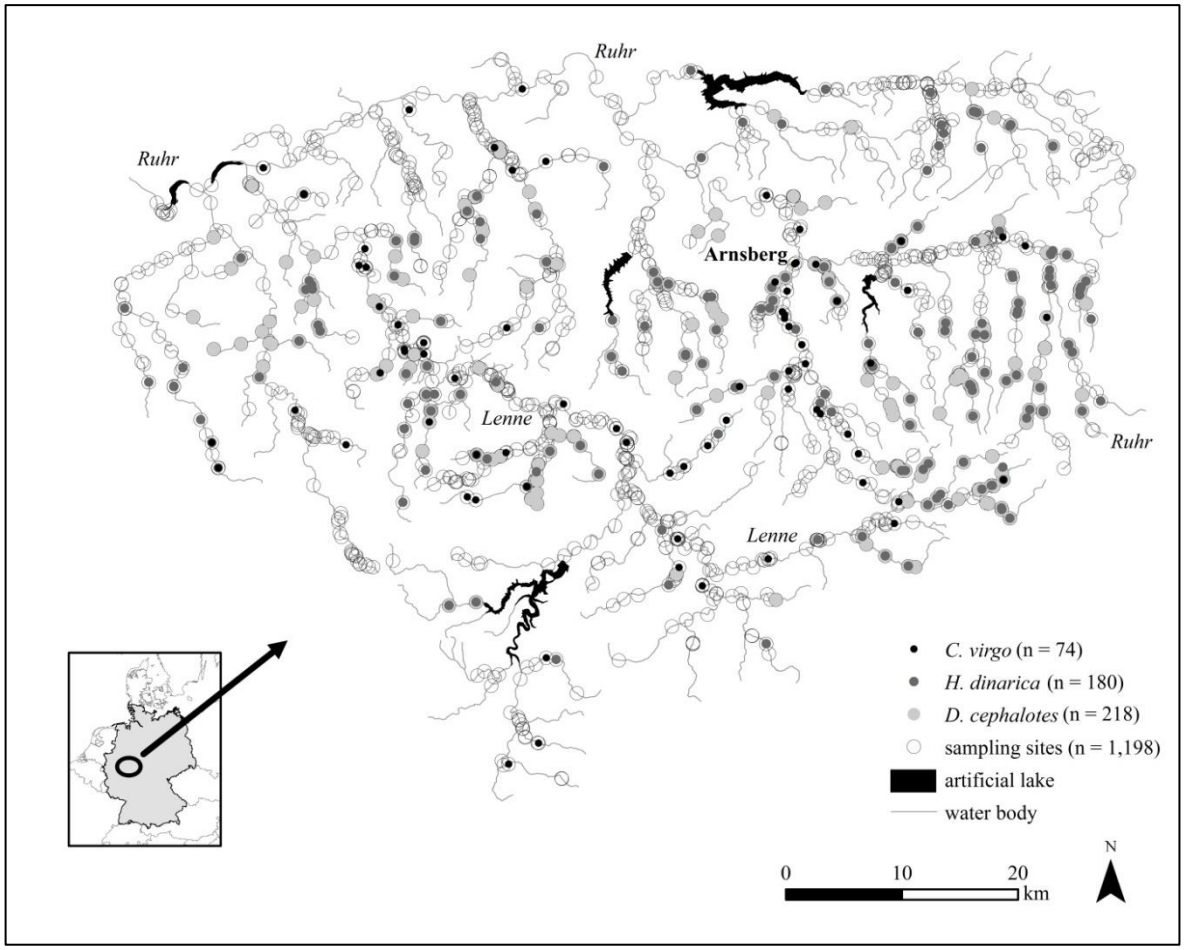

Figure 3: Study area with recorded source populations; total number of sites = 1,198. The data were derived from our own field data (n = 225), Dangel (personal communication) (n = 6), Frenz & Hering (2000) (n = 31), LANUV NRW (unpublished data) (n = 546), Maue (2006) (n = 6), Podraza et al. (2005) (n = 72), Rudolph (2011) (n = 7) and Ruhrverband (unpublished data) (n = 305).

We addressed three model species: *Calopteryx virgo* Linnaeus 1758 (Odonata; Calopterygidae), *Dinocras cephalotes* Curtis 1827 (Plecoptera; Perlidae) and *Hydropsyche dinarica* Marinkovic 1979 (Trichoptera; Hydropsychidae), each of them representing different dispersal capabilities. *Calopteryx virgo* (prevalence: 6%; see Figure 3) is a good flyer, but relatively immobile as larvae. Adults of *D. cephalotes* (prevalence: 18%) are more sedentary with a mobile aquatic stage. *Hydropsyche dinarica* (prevalence: 15%) is highly mobile in both the larval and adult stages.

Potential in-stream dispersal barriers (dams, weirs, impoundments, culverts) and terrestrial dispersal barriers (urban land use, road infrastructure, coniferous and deciduous or mixed forest cover, open land, degraded riparian vegetation) were

derived from the physical habitat survey of the Federal State of North Rhine-Westphalia (MUNLV-NRW 2003), a record of transverse barrier structures (e.g., weirs) (Anderer et al. 2007) and a fine-scale land cover survey (LANUV NRW © Fachdaten; see Afflerbach & Kunze 2006; spatial grain: 5 × 5 m) (Table 1).

Table 1: Data sources used to identify and parameterise dispersal barriers.

Data	Source	Reference	Description	Landscape elements
Land use	ATKIS basic DLM 2007	Afflerbach & Kunze (2006)	46 different land use categories; spatial grain: 5 × 5 m	cover of deciduous, coniferous and mixed forest, open land, urban area, road infrastructure, water body, impounded water bodies
Physical habitat survey	"Gewässer-strukturgüte-kartierung vor-Ort-Verfahren"	MUNLV-NRW (2003)	30 hydromorpho-logical and habitat parameters; stretch length: 100-800 m	Composition of riparian vegetation; Presence of culverts
Trans-verse structures	"Querbau-werke-Informations-system NRW"	Anderer et al. (2007)	Point coordinates for 2,875 transverse structures in the study area	Presence of weirs and groundsills, classified as relevant dispersal barriers by the authors (n = 848)

2.2.2. The least-cost modelling approach

2.2.2.1. Dispersal model

We applied a least-cost algorithm that identifies the lowest accumulated (friction) cost between any grid cell and the surrounding source grid cells (here, the known presences of the model species) in a grid (Adriaensen et al. 2003, Dedecker et al. 2007). We preferred the least-cost approach over others (e.g., Euclidean distance), since it allowed us to easily add and analyse the costs imposed by in-stream and terrestrial landscape barriers. Such barriers are usually excluded from studies using Euclidean distance (e.g., Keller & Holderegger 2013).

The algorithm is implemented in the tools *Cost Distance* (ESRI 2011a) and *Path Distance* (ESRI 2011b), both of which are part of the Spatial Analyst extension of ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). With *Cost Distance* we addressed the potentially undirected dispersal of adult aquatic insects, while we handled the

directed aquatic upstream and downstream dispersal of larvae with *Past Distance* (Figure 4). The latter requires a directed river network (with flow directions). This was achieved by splitting the river network into segments, coding these segments with continuously decreasing values from the source to the mouth, and further processing the segmented network using the ArcGIS tool *Flow Direction* (ESRI 2011c).

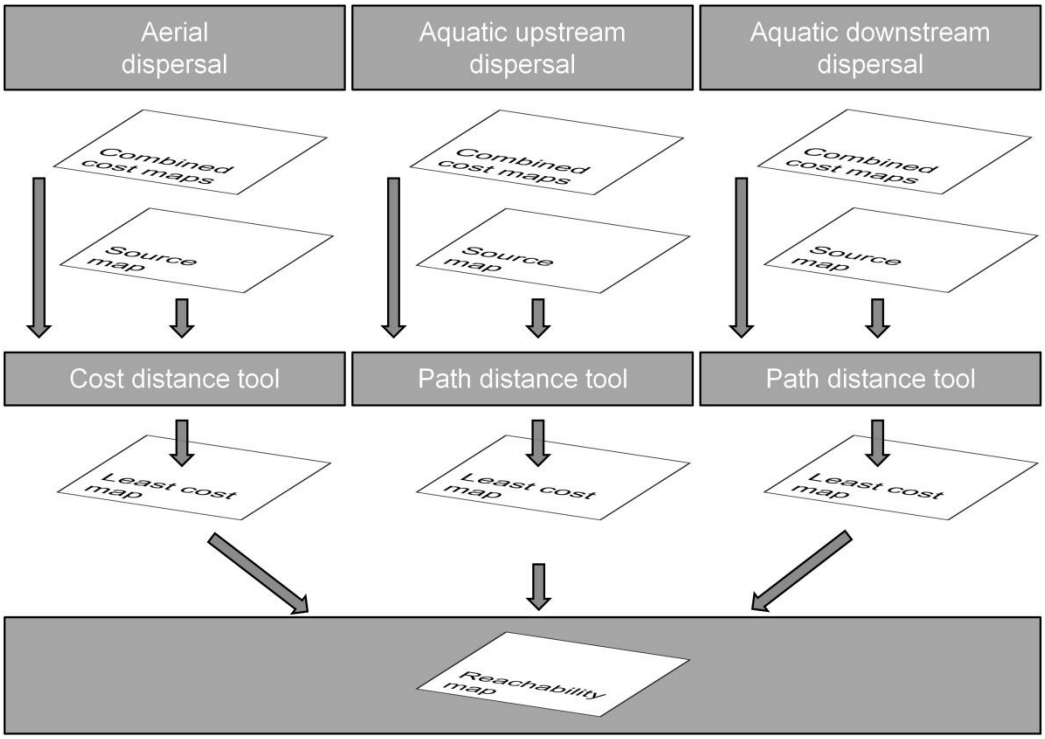

Figure 4: Conceptual framework of the least-cost modelling approach applied in this study for each species.

The actual species distribution (derived from 1,198 sites) was mapped on a 5 × 5 m grid and provided the basis for dispersal modelling. For each species and dispersal mechanism a combined friction cost map was derived from the source data (Table 1) and the assigned friction cost values (Table 4). The fine spatial grain (5 × 5 m) allowed to distinguish individual weirs or other small barrier elements. Linear barriers (e.g., weirs) were arbitrarily set to a width of 12 m to ensure that these barriers cover the river network and are interpreted as barriers within *Path Distance* (Adriaensen et al. 2003).

The lowest accumulated friction cost of each grid cell was then calculated separately for each species and dispersal mechanism. The resulting least-cost

maps allowed to compare the distances travelled by larvae (up-/downstream) and by adults and thus enabled comparisons of larval and terrestrial dispersal. Further, the least-cost maps were combined for each species by the ArcGIS tool *Combine* (ESRI 2011d). This allowed to identify the grid cells that are potentially reachable and therefore colonisable through any dispersal mechanism within one life cycle of the respective species.

2.2.2.2. Dispersal data and dispersal costs

Individual dispersal capabilities can be expressed as a mean or maximum distance that a specimen can disperse within each stage of its life cycle. Here, we selected a progressive approach based on maximum dispersal distances, which were derived from a review of the literature and expert knowledge (Table 2).

Table 2: Maximum dispersal distances (m) per life cycle estimated by the authors and applied in this study for *Hydropsyche dinarica*, *Calopteryx virgo* and *Dinocras cephalotes*. Recommended references are marked by footnotes.

Species	**Aerial dispersal (m)**	**Aquatic upstream dispersal (m)**	**Aquatic downstream dispersal (m)**
H. dinarica	5,000[a, b, c, d, e, f, g]	850[a, f, h, i]	500[a, f, i]
C. virgo	4,000[a, f, j, k]	30[a, f, k]	50[a, f, k, l, m]
D. cephalotes	500[a, n, o]	300[a, p]	300[a]

[a] = Bis & Usseglio-Polatera (2004), [c] = Coutant (1982), [c] = Ehlert (2009), [d] = Kovats et al. (1996), [e] = Malicky (1987), [f] = Poff et al. (2006), [g] = Schuhmacher (1970), [h] = Gellert (2011), [i] = Schuhmacher (1969), [j] = Stettmer (1996), [k] = Vieira et al. (2006), [l] = Carvalho & Uieda (2006), [m] = Dorier & Vaillant (1954) in Ward & Mill (2007), [n] = Fochetti (pers. obs.) in Ketmaier et al. (2001), [o] = Rupprecht (2009), [p] = Schwarz (1970).

This review included more than 150 references that deal with dispersal of benthic invertebrates (Appendix: Table A1). The recent knowledge on species dispersal was aggregated with focus on reported dispersal distances and physical in-stream and terrestrial dispersal barriers. The references covered a wide range of publication types from articles published in peer-reviewed journals, other journals, dissertations, diploma-theses to posters, presented at scientific conferences. We are aware of the potential overestimation of dispersal distances linked to this approach, but agree with Keller & Holderegger (2013) that maximum distances can be decisive for the recolonisation of river sections. Further, the lack of

quantitative dispersal data did not allow of the calculation of mean or median values with most species.

The barrier effect that a specific in-stream or terrestrial landscape element imposes on a species' dispersal can be expressed as (friction) costs. In the case of merolimnic species, a natural (highly permeable) stream corridor imposes only minor costs on larval and adult dispersal. In contrast, barriers, like large weirs or dams within the stream continuum, can imply huge costs, that may hinder or even block larval dispersal. The assignment of friction costs was primarily based on expert knowledge and assisted by studies providing qualitative information on the barrier effects of in-stream and terrestrial landscape elements (Table 3).

For all relevant landscape elements, friction costs per meter were estimated based on an arbitrary set of five values (1; 2; 5; 10; 10,000; Table 4). In addition to Dedecker et al. (2007), who related the friction costs for different landscape elements to each other, we also related the friction costs to the maximum dispersal distance within a dispersal mechanism. This maximum dispersal distance constituted the budget for accumulated friction costs across landscape. For example, the maximum aerial dispersal distance of *H. dinarica* (4,000 m, Table 2) translates into a friction cost budget of 4,000 for aerial dispersal. Therefore, the maximum dispersal distances were only facilitated by a friction cost value of one per meter across these distances. Absolute barriers were assigned the highest cost value (10,000), exceeding the budget for friction costs to cross one meter. Partly permeable landscape elements were classified with intermediate friction cost values (2, 5 or 10), that translate equivalently into 50%, 20% or 10% of potential maximum dispersal distance within that landscape element. For example, the potential dispersal distance of *H. dinarica* decreases from 4,000 m to 400 m through urban area with a friction cost value of 10 (Table 4).

Table 3: Hindering (−) and facilitating (+) landscape elements for three different dispersal modes of *Calopteryx virgo* (CVIR), *Dinocras cephalotes* (DCEP) and *Hydropsyche dinarica* (HDIN). The classification was based upon expert and literature knowledge; n. rel. = not relevant for dispersal.

	Landscape elements	**Aerial dispersal**			**Aquatic upstream dispersal**			**Aquatic downstream dispersal**		
		CVIR	DCEP	HDIN	CVIR	DCEP	HDIN	CVIR	DCEP	HDIN
Land use	Deciduous and mixed forest	–[a]	+[b, c]	+	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Coniferous forest	–[a]	–[d, e]	–[e]	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Open land	+[a, f, g]	–	–	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Urban area	–[h]	–[h]	–[i, h]	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Road infrastructure	–	–	–	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
Water body	Near natural riparian vegetation	+[j]	+	+[k]	+	+	+	+	+	+
	Degraded riparian vegetation	–[j]	–	+	+	+	+	+	+	+
	Impounded water body > 1,000 m^2	+	+	–[l, m]	–	–	–[n]	–	–[o, p]	–[o, p]
	Transverse barriers (e.g., weirs)	n. rel.	n. rel.	n. rel.	–	–	–	–	–	–
	Culverts	–[j]	–	–[q]	–	–	–	–	–	–

[a] = Keller et al. (2012), [b] = Macneale et al. (2005), [c] = Winterbourn et al. (2007), [d] = Briers et al. (2002), [e] = Hering (1992), [f] = Pither & Taylor (1998), [g] = Stettmer (1996), [h] = Smith et al. (2009), [i] = Smith & Collier (2001), [j] = Sternberg & Buchwald (1999), [k] = Ehlert (2009), [l] = Statzner (1978), [m] = Ulfstrand (1970), [n] = Schuhmacher (1969), [o] = Vinikour (1980), [p] = Vinikour (1981), [q] = Blakely et al. (2006).

Table 4: Dispersal costs for three different dispersal modes of *Calopteryx virgo* (CVIR), *Dinocras cephalotes* (DCEP) and *Hydropsyche dinarica* (HDIN). Costs were derived from the information listed in Table 3; n. rel. = not relevant.

	Landscape elements	**Aerial friction costs (cost units m^{-1})**			**Aquatic upstream friction costs (cost units m^{-1})**			**Aquatic downstream friction costs (cost units m^{-1})**		
		CVIR	DCEP	HDIN	CVIR	DCEP	HDIN	CVIR	DCEP	HDIN
Land use	Deciduous and mixed forest	5	1	1	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Coniferous forest	10	10	5	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Open land	1	5	1	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Urban area	10	10	10	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
	Road infrastructure	10	10	10	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.	n. rel.
Water body	Near natural riparian vegetation	1	1	1	1	1	1	1	1	1
	Degraded riparian vegetation	5	5	1	1	1	1	1	1	1
	Impounded water body > 1,000 m^2	1	1	5	2	5	5	2	5	5
	Transverse barriers (e.g., weirs)	n. rel.	n. rel.	n. rel.	10,000	10,000	10,000	5	5	5
	Culverts	10	10	10	2	2	2	1	1	1

In contrast to Dedecker et al. (2007), we limited our predictions to a single life cycle period, including the adult stage (aerial dispersal) only once in the calculation. Modelling continuous and additive dispersal over two or more life cycles is required, if species' dispersal is still in progress, i.e., for invasive species. The species in this study are assumed to have colonised every suitable habitat that is not blocked by dispersal barriers, during the last decades.

Three dispersal mechanisms were distinguished: aerial (adult) dispersal, active aquatic (larval) upstream dispersal and active/passive aquatic (larval) downstream dispersal. Although larval drift was accounted for, we had to excluded "catastrophic" drift (in course of flash floods) and zoochorie (e.g. via water birds; Figuerola & Green 2002) from our models, due to the lack of information on the distances dispersed via these pathways in the literature.

2.2.3. Model validation

Dispersal models and the resulting predicted reachability of stream stretches were validated following two scenarios: i) with barriers in the model and ii) without barriers in the model. For the latter, all friction costs in the model were set to one. The validation procedure was based on elements of the confusion matrix (Fielding & Bell 1997), i.e., on the comparison of correctly classified absences of species. Nevertheless, the detection of true positives (TP; species observed and predicted by dispersal models to be present) and false negatives (FN; species observed, but not predicted by dispersal models to be present) was limited by the fact that all known presences of the species were used as starting points for the modelling procedure. By definition, TP was 100%. Therefore, the validation of dispersal models considered only the cases with observed absences, i.e., the true negatives (TN; species not observed and not predicted by dispersal models to be present) and false positives (FP; species not observed, but predicted by dispersal models to be present). Additionally, we excluded sites from the validation procedure that provide unsuitable habitat conditions, to disentangle habitat constraints from dispersal constraints in their effect on species absences. Habitat constraints are one major factor explaining species absences that are called "environmental absences" (Lobo et al. 2010). For example, a species might be able to reach a certain site but not establish a population due to habitat

constraints. The remaining sites with “contingent absences” (Lobo et al. 2010) are assumed to be not colonised due to other factors, e.g. dispersal constraints, rather than habitat constraints.

To estimate which sampling sites provide suitable habitat conditions, we conducted a logistic regression for each species. Logistic regression with forward selection of predictors was performed with SPSS 20.0 (IBM). The cutoff-value for habitat suitability classification was set, where true skill statistic (TSS) is maximised. TSS (= Sensitivity + Specificity – 1) was chosen, because species’ prevalence is below 50% and TSS is independent from species prevalence (Allouche et al. 2006). TSS was calculated upon Sensitivity and Specificity, that were derived for 101 cutoff-values (0.00, 0.01, 0.02,…1.00) in R (R Core Team 2014) using the package “PresenceAbsence” (release 1.1.9) (Freeman & Moisen 2008). We chose the sampling sites from 2010 (n = 121), as described above, to conduct the logistic regression analysis. For validation purposes Nagelkerke’s R^2 (Nagelkerke 1991) was calculated. Additionally, positive predictive power and correct classification rate (Fielding & Bell 1997) were calculated upon a “prospective sampling” data set (Fielding & Bell 1997) with 104 samples from 2011. For each species the resulting logistic regression was finally applied to 1,093 out of 1,198 sample sites that are described above. For these sites environmental variables were available.

We chose a set of 27 environmental variables (Table 5) based on Gies et al. (2015a). Fifteen environmental variables covered river course, longitudinal profile, cross section, bank and bed structure and riparian area. Physical habitat parameters (MUNLV-NRW 2003) were complemented by riparian land cover using high-resolution remote sensing data (LANUV NRW © Fachdaten; spatial grain: 5 × 5 m). Therefore, two riparian areas (20 m and 200 m total width, 1,000 m length) were delineated for each sample section in a GIS system and then clipped with land cover data. For each riparian area, we calculated percent cover of five land use types: cropland, non-intensive land use (i.e., grassland, parks, etc.), deciduous forest, coniferous/mixed forest and urban/industrial areas. In addition, we calculated the quotient of forested area in the 20 m buffer and intensively used areas (cropland, urban/industrial areas) in the 200 m buffer. This quotient is meant to represent the potential riparian buffer capacity against chemical pressures of

adjacent land uses. Altitude (m a.s.l.) and distance to source (m) were chosen as proxy for the longitudinal zonation of each sample site. Altitude was derived from a digital elevation model (DGM 5; spatial grain: 10 × 10 m) and distance to source was calculated upon a river network (Gewässernetz NRW 3a) with ArcGIS (ESRI).

Table 5: Environmental variables on longitudinal zonation, hydromorphology and riparian land use which were included into the distribution modelling procedure. Longitudinal zonation proxies are based on a german digital elevation model (DGM 5) and a fine scale river network (Gewässernetz 3a). Hydromorphological variables are based on the German physical habitat quality survey that includes structural in-stream variables as well as variables on the riparian condition. Riparian land use variables are based on the German Topographical Cartographic Information System (ATKIS basis DLM 2007).

	Environmental parameters		**Abbreviation**
Longitudinal zonation	Altitude a.s.l. (m)		Altitude
	Distance to source (m)		DistSource
Physical habitat quality	Planform		PlanForm
	Erosion at bends		Erosion
	Features indicating natural channel dynamics (e.g., wood jams)		FeatDyn
	Riffels and steps		Riffles
	Flow diversity		FlowDiv
	Depth variability		DepVar
	Substrate diversity		Subsdiv
	Channel features (e.g., backwater pools, rapids)		FeatChan
	Cross-section form		CrSecForm
	Cross-section depth		CrSecDep
	Bank erosion (indicating widening of channel)		BankEro
	Cross-section width variability		CrSecWid
	Riparian vegetation		RipVeg
	Bank protection		BankProt
	Bank features (e.g., woody debris, undercut banks)		FeatBank
Land use categories	Cropland (%)	100 m on either bank side (wide)	Crop_w
	Extensive/pasture (%)	10 m on either bank side (narrow)	Ext_n
		100 m on either bank side (wide)	Ext_w
	Deciduous forest (%)	10 m on either bank side (narrow)	DecFor_n
		100 m on either bank side (wide)	DecFor_w
	Coniferous/mixed forest (%)	10 m on either bank side (narrow)	ConFor_n
		100 m on either bank side (wide)	ConFor_w
	Urban/industrial area (%)	10 m on either bank side (narrow)	Urb_n
		100 m on either bank side (wide)	Urb_w
	Index of riparian buffer capacity	Ratio of (forested area in 20 m buffer) / (urban and cropland area in 200 m buffer + 10,000)	F020U200

2.3. Results

Hydropsyche dinarica was found at 180 locations in the Ruhr catchment; from these sites, we predicted that the species is able to reach nearly two thirds of all

river sections in the model catchment (= 67%, Figure 5 A, Table 3). *Calopteryx virgo*, present at only 74 sites, is able to reach 27% of the catchment (Figure 5 B). *Dinocras cephalotes*, though present at the largest number of sites (218), is predicted to be able to reach only 9% of the catchment within a single life cycle (Figure 5 C).

Aerial dispersal accounted for all (*C. virgo*) or at least the largest part (*H. dinarica*, *D. cephalotes*) of the total reachable river length (Table 6). In contrast, only 10%, 0.3% and 6% of the river sections were reachable by the larvae of *H. dinarica*, *C. virgo* and *D. cephalotes*, respectively, if larval dispersal was considered under the presence of dispersal barriers (weirs, etc.).

In contrast to the dispersal models “with barriers”, i.e., with landscape friction costs and in-stream barrier structures, the scenario “without barriers” led to uniformly shaped areas of reachability around each source population (Figure 5 A–C). The plots correspond to equal friction costs assigned to every grid cell in the landscape and result in a total reachable river length of 1,485 km (81% of the entire model catchment) for *H. dinarica*, 820 km (45%) for *C. virgo* and 213 km (12%) for *D.* cephalotes (Table 6) within a single life cycle. This translates to an increase in reachable river length of about 21% (*H. dinarica*), 36% (*D. cephalotes*) and 63% (*C. virgo*) compared to the scenario that considers barrier effects. The differences between the two scenarios were most pronounced for aerial dispersal (21 to 63% relative increase in reachability, when barriers are not considered), whereas the corresponding values ranged from 1 to 13% for aquatic dispersal.

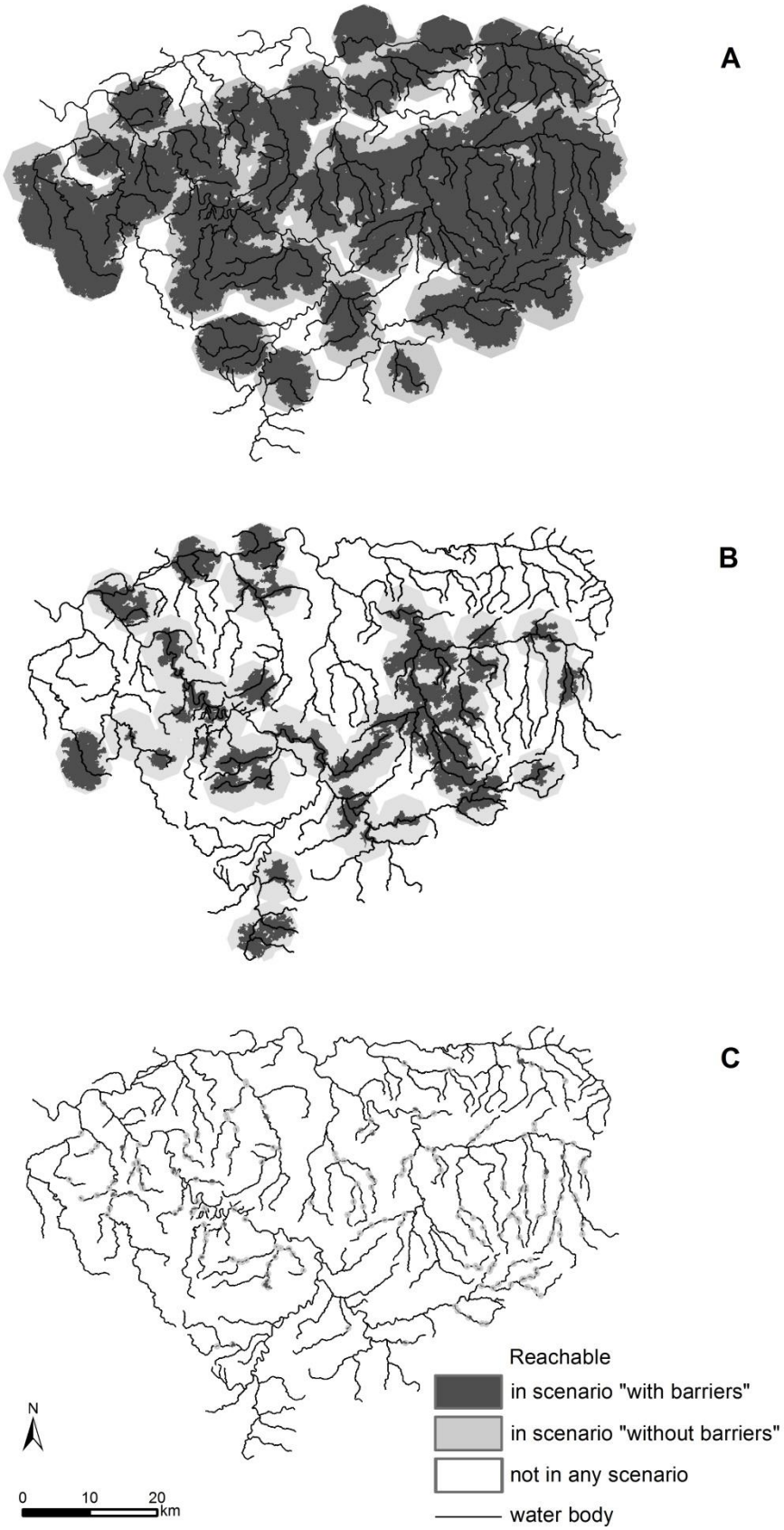

Figure 5: Dispersal map with reachable river stretches for *Hydropsyche dinarica* (A), *Calopteryx virgo* (B), *Dinocras cephalotes* (C) indicated for the scenarios “with barriers” and “without barriers”.

Table 6: For each dispersal mode, the reachable river length (km), the relative proportion of total river length (abs.%) and the difference in reachable river length between both scenarios (Δ rel.%) are indicated (total length of rivers in the model catchment = 1,832 km).

Species	**total**			**aerial**			**aquatic upstream**			**aquatic downstream**		
	km	abs.%	Δ rel.%	km	abs.%	Δ rel.%	km	abs.%	Δ rel.%	km	abs.%	Δ rel.%
"with barriers"												
H. dinarica	1,224	67	-18	1,224	67	-18	113	6	-11	73	4	-1.4
C. virgo	503	27	-39	503	27	-39	3	0.1	-1	4	0.2	-1.5
D. cephalotes	157	9	-27	144	8	-33	54	3	-5	56	3	-1.2
"without barriers"												
H. dinarica	1,485	81	+21	1,485	81	+21	128	7	+13	74	4	+1.4
C. virgo	820	45	+63	820	45	+63	3	0.1	+1	4	0.2	+1.5
D. cephalotes	213	12	+36	213	12	+49	57	3	+5	56	3	+1.2

The comparison of aquatic upstream and downstream dispersal between the two scenarios suggests that barriers affect the upstream dispersal of *H. dinarica* most strongly (+13% relative increase in reachability). Only a minor change of a maximum of +7% was calculated for the other species (Table 6). Therefore in-stream barriers tend to have a minor impact on the modelled aquatic dispersal patterns.

Results from logistic regressions were modest and varied between species with a N-R^2 ranging from 0.251 to 0.351, correct classification rates ranging from 65 to 69% and positive predictive power ranging from 40 to 58% (Table 7). From a total of 1,093 sites 339, 305 and 538 sites were not colonised but predicted to provide habitat conditions for *D. cephalotes*, *H. dinarica* and *C. virgo*, respectively. Upon these sites the dispersal models were validated.

Table 7: Results of logistic regression analysis including Nagelkerke's R^2 (N-R^2), environmental predictors and their coefficient. Model accuracy was assessed with positive predictive power and correct classification rate (Fielding & Bell 1997).

Response variable	**N-R^2**	**Regression constant**	**Regression coefficient**	**Predictors**	**Positive predictive power (%)**	**Correct classi-fication rate (%)**
H. dinarica	0.351	-4.024	2.330	F020U200	40	65
			0.403	RipVeg		
C. virgo	0.215	4.790	-0.006	Altitude	44	69
			-0.032	ConFor_n		
			-0.926	FlowDiv		
D. cephalotes	0.309	-0.729	-0.000076	DistSource	58	68
			1.053	F020U200		

The number of true negative (TN) predictions increased from *H. dinarica* (34% true negative rate) over *C. virgo* (59%) to *D. cephalotes* (93%), whereas FP rates were 66%, 41% and 7%, respectively, for the three species (Figure 6).

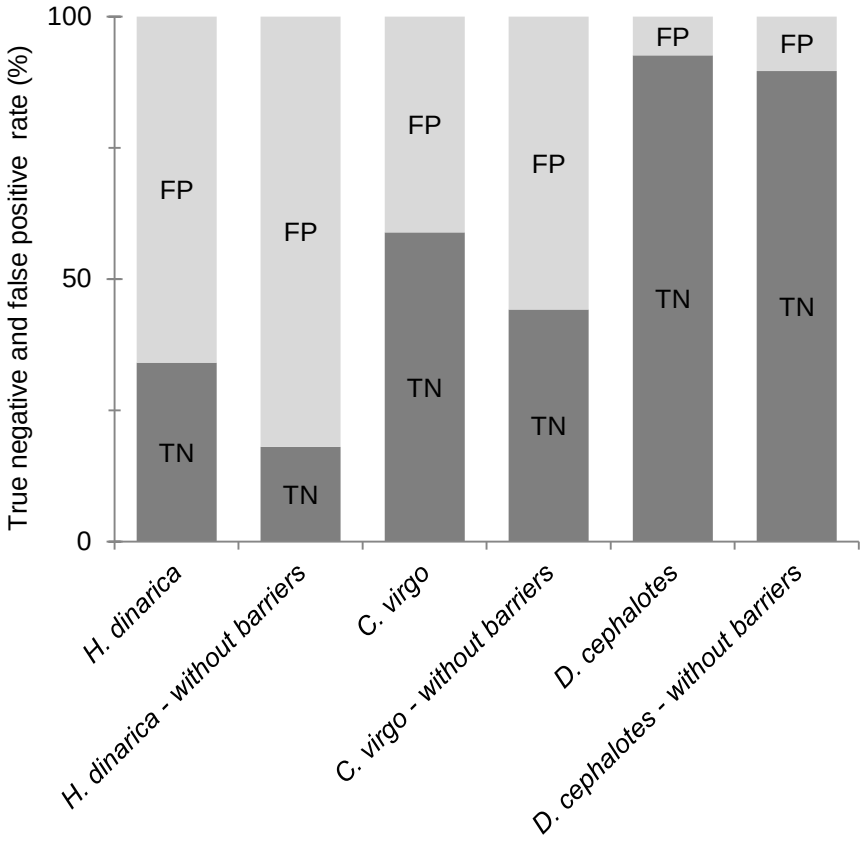

Figure 6: True negative (TN) and false positive (FP) rate (%) for sampling sites with predicted suitable habitats but observed absences of *Hydropsyche dinarica* (n = 305), *Calopteryx virgo* (n = 538) and *Dinocras cephalotes* (n = 339) for the scenarios “with barriers” and “without barriers”.

Notably, for the dispersal model of *H. dinarica* the rate of TN predictions decreased from 34% (scenario “with barriers”) to 18% (scenario “without barriers”). The rate of FP predictions correspondingly increased, from 66% (“with barriers”) to 82% (“without barriers”) (Figure 6). These differences were also pronounced for *C. virgo*, which revealed a 15%-point decrease and 15%-point increase in TN and FP rates respectively from “with barriers” to “without barriers”. The difference, however, was almost negligible for *D. cephalotes*, with only a 3%-point decrease in performance.

2.4. Discussion

2.4.1. Methodological considerations

2.4.1.1. Dispersal modelling using the least-cost approach

For a reliable application of the least-cost approach, it is crucial to know i) the current distribution of source populations of the target species, ii) their specific dispersal capabilities (i.e., distances travelled in time as larvae and adults) and iii) the barrier effects that in-stream and terrestrial landscape structures could impose. The current species distribution was not derived from a recent sampling but from a data set that spans over several years. Therefore, the knowledge on the current distribution of source population might be inaccurate. But we expect that the distribution of species did not change considerably within the last years because the habitat conditions in the study area did not change drastically in this time span (AWWR & Ruhrverband 2012). Given the dense coverage of nearly 1,200 sampling sites (Figure 3), the current distribution of source populations of the three model species was derived in a fine spatial grain. Certainly, not every source population, that was actually present in the study area, is likely to be represented by our data. Yet, median distance between any river stretch and its closest sampling site potentially colonisable by target species was only 561 m. As this falls almost entirely within the range of the aerial dispersal capabilities of the three model species (Table 2), we believe that our data sufficiently fit the catchment-wide least-cost approach. Nevertheless, we can assume that the amount of predicted reachable river stretches would increase, if we knew every present source population.

Less reliable, however, is the current knowledge about the dispersal distances of the larval and adult stages of the three model species, although there is some empirical evidence available in the literature (Table 2). Like in other comparable studies (Koen et al. 2012), the values in our study can only represent single findings and expert opinions without statistical rigor. Further, dispersal distances are likely to be subject to intraspecific variation; it is likely that not all individuals within populations are good “dispersers”. Observed dispersal distances, for example, may refer to a relatively small number of individuals (Stettmer 1996) and

may have missed long-distance dispersers. Moreover, we have to state that the predicted dispersal range is likely overestimating species' dispersal, because the underlying least-cost algorithm assumes that species are first aware of the dispersal costs of the surrounding landscape and secondly choose the least costly route to get to a site (Baguette & Van Dyck 2007).

The friction costs that in-stream and terrestrial landscape structures may impose on aquatic and aerial dispersal constitute the most critical requirement for reliable dispersal modelling (Adriaensen et al. 2003, Dedecker et al. 2007). Dedecker et al. (2007) have already noted the lack of sufficient empirical data to support the quantification of the barrier effects of certain river or landscape structures (see also Smith et al. 2009, Vaughan 2002). Here, we followed a qualitative approach and classified friction costs into five cost groups based on the qualitative information available in the literature, as outlined in Table 3. The two extreme groups (1 and 10,000) represent "no barrier" and "total barrier", which we believe can be reliably assigned to grid cells without any barrier structure and to grid cells with strong barriers (e.g., dams, weirs, urban areas), respectively. Due to this large difference between the extreme groups, the three intermediate groups 2, 5 and 10 are of minor importance in the presence of barriers, which renders our approach rather conservative in terms of the allocation of friction costs. Dispersal capabilities may have been overestimated for river sections and scenarios without barriers, yet it is unlikely that the limiting effect of dispersal barriers has been underestimated. Further, lateral aerial dispersal is species-specific (see Macneale et al. 2005) and may be constrained to the stream corridor (Petersen et al. 2004) or not (Didham et al. 2012, Landeiro et al. 2011). Because no constraints were reported for the three model species, we did not in fact limit aerial dispersal to the stream corridor in our models.

2.4.1.2. Model validation

The application of a confusion matrix to a dispersal model assumes that the presence / absence of a species at a given site is exclusively determined by dispersal. It fully neglects other factors determining species occurrence, such as habitat suitability. We excluded "environmental absences" (Lobo et al. 2010), that can be explained with habitat constraints and restricted our validation approach to sites with absences, that are predicted to provide suitable habitats. Nevertheless,

we need to stress that species absences may also be caused by the presence of competitive species already holding niches (“contingent absences”). Species absences may also result from sampling errors, e.g., if a species is being overlooked at a site (“methodological absences”) (Lobo et al. 2010). While we consider the latter unlikely in our own samples, which were collected with considerable effort to find the species, it might be more likely in the samples resulting from “Multi-Habitat-Sampling”.

Sample sites with suitable habitats were identified by logistic regression models. Still, the performance of logistic regression models, e.g., positive predictive power, was only modest. Only 40%, 44% and 58% of predicted presences were truly observed for *H. dinarica*, *C. virgo* and *D. cephalotes*, respectively. This translates into a certain amount of predicted suitable habitats that are to be considered as non-suitable habitats in reality. Therefore, some sample sites, that are included in the validation procedure for the dispersal models, may still be constrained by habitat constraints rather than dispersal limitations.

The validation of logistic regressions was based upon a subset (n = 104) of the available data set (n = 1,093), because the information on the presence / absence of species were considered to be more reliable for our own samples, as mentioned above. Additionally, the usage of the entire data set as a training data set for logistic regression models would have interfered with our purpose to disentangle confounding habitat constraints from dispersal constraints prior to dispersal model validation. As logistic regression analysis relates species presence and absence to environmental predictors, predictions of habitat suitability might be biased by dispersal limitations, increasing the numbers of sample sites that are falsely predicted as non-suitable habitats due to ongoing dispersal constraints.

The two elements of the confusion matrix used here, TN and FP, revealed high model validity for the dispersal model of *D. cephalotes*, and less validity for the other two species. Our percentage of actual absences correctly predicted by dispersal models as absences (TN rate or specificity) ranges from 34 to 93%. This range is comparable to model performances in studies dealing with species distribution models based on habitat parameters, with a specificity ranging from 70 to 85% for plant species (Liu et al. 2005) or from 50 to 90% for aquatic invertebrates (Manel et al. 2001). Nevertheless, it is not our goal to prove the

validity of the developed dispersal models in general, but to test if the consideration of dispersal barriers improves the validity of dispersal models.

TN and FP revealed higher model validity for species with lower dispersal capabilities. This finding suggests that the dispersal capabilities of *C. virgo* and *H. dinarica* might have been overestimated, either because the distances as reported in the literature overestimate the species' actual capabilities or because the costs allocated to in-stream and terrestrial structures do not reflect actual friction costs very well.

In summary, our model approach tends to overestimate the dispersal of strong dispersers within one generation, which requires further field surveys to determine the actual distances travelled by the model species within the frame of one life cycle. Further efforts are also required to better parameterise the friction costs imposed by potential in-stream and terrestrial landscape barrier structures.

2.4.2. The role of species dispersal capabilities and prevalence

The share of reachable river sections was more strongly related to the dispersal capabilities than to the prevalence of the model species (Table 2). The prevalence of the three species increased in the order: *Calopteryx virgo* < *H. dinarica* < *D. cephalotes*, whereas the reachable river sections increased from *D. cephalotes* < *C. virgo* < *H. dinarica.* Therefore, dispersal capability is very likely to be dominated by aerial dispersal, which is the most important mechanism in the cases of the three model species (Table 2) and for many other aquatic insects with winged adult stages (Hughes et al. 2008). Furthermore, aerial dispersal is not restricted to the dendritic network of stream corridors (Didham et al. 2012, Landeiro et al. 2011, Macneale et al. 2005). Surrounding streams can be reached by lateral dispersal often at much shorter distances compared to the alternative dispersal route alongside stream corridors (compare Fagan 2002). In terms of time, aerial dispersal could require a longer period to enable the recolonisation of a site compared to aquatic upstream or downstream dispersal (Spänhoff & Arle 2007). Yet, catastrophic drift needs to be considered in dispersal over longer distances downstream, which was not addressed in our study.

In restoration management, decisions for potential restoration sites could be based either on a progressive modelling approach (maximum distances) or a conservative approach (median distances). The more progressive the approach, the more time it will take until species establish new populations within the predicted dispersal range and variety of habitats; vice versa, the more conservative approach, the less time will pass until restored sites within the predicted dispersal range will be colonised. In this study we applied maximum distances and therefore colonisation within the predicted range will be more time consuming.

2.4.3. The effect of dispersal barriers

Overall, we found terrestrial landscape barriers to impact dispersal much more than in-stream barriers. This is because the adult (winged) stages of many aquatic insects are expected to disperse much better than their aquatic larvae. Yet, until now, little is known about the landscape filters that specific landscape structures may constitute for dispersal of aquatic insects.

Least-cost modelling is well suited for the analysis of the potential filter effects of such structures (e.g., Dedecker et al. 2007) and offers a powerful tool with which to compare the outcomes of different scenarios, for example, with and without barriers, as applied in our study. Despite uncertainties concerning the dispersal costs posed by individual landscape structures and dispersal distances, the comparison of different scenarios can help reveal the relative importance of dispersal parameters or landscape structures.

The comparison of two scenarios – with and without barriers – revealed notable differences: up to 63% more river sections (*C. virgo*) were reachable by the model species if barriers were not included in the model. Second, the two elements of the confusion matrix used here, TN and FP, revealed higher model validity for every dispersal model “with barriers”. In agreement with Galic et al. (2013), this highlights the potential role of dispersal barriers for aquatic insects and points at the need to include dispersal barriers in the models.

The prediction of reachable river sections depends strongly on the parameters’ maximum dispersal distance and the assigned cost value. Especially for aerial

dispersal, the predicted dispersal range varies strongly with the assumed maximum aerial dispersal distance. Given the radial shape of aerial dispersal range, we can expect that a doubling of the assumed dispersal distance results in a more or less fourfold area of dispersal range. Besides this, aerial dispersal is the most prominent and most impacted dispersal mechanism by barriers for all three species in this study, which shows us that this is the most sensitive dispersal mechanism in our modelling approach. Moreover, we found that the scenario “with barriers” revealed higher model validity for all three species, indicating that this finding is robust and may be valid for many other aquatic insects.

These findings are in agreement with Michels et al. (2001), who found that Euclidean distance is less appropriate than measures incorporating hindering and facilitating landscape elements for explaining the genetic similarity of zooplankton populations in interconnected ponds and with Ray et al. (2002), who revealed circular distances to be less appropriate than friction-based distances in the prediction of toad occurrences. In contrast, some aquatic insect species groups, e.g., Odonates, are capable of rare long distance dispersal as adults (May 2013, Russell et al. 1998). Within these long distance dispersal events, landscape dispersal barriers might impose less costs on the dispersal. For example, Keller & Holderegger (2013) found least-cost modelling to be appropriate for short dispersal distances of *Coenagrion mercuriale* (Odonata), whereas long distance dispersal was better explained with Euclidean distance. However, this could have been caused by limiting least-cost modelling to the stream corridor, whereas lateral dispersal, e.g., through facilitating dispersal landscape structures like open land (Keller et al. 2012), was only considered with Euclidean distance in this study.

3. Application and validation of a new approach for modelling benthic invertebrate dispersal: first colonisation of a former open sewer system

3.1. Introduction

Freshwater systems are among the most strongly impacted ecosystems by humans (Sala et al. 2000) due to multiple human water uses (e.g., water withdrawal, transport, damming and recreation). These impacts lead to habitat fragmentation and reductions in biodiversity, with the extinction rate of freshwater species estimated to be as much as five times higher than for terrestrial species (Ricciardi & Rasmussen 1999, Riis & Sand-Jensen 2001). Numerous restoration projects have been implemented in the last few decades (e.g., Bernhardt et al. 2005, Bernhardt et al. 2007, Feld et al. 2011) to improve the status of aquatic ecosystems and maintain biodiversity. Yet, morphological restorations (e.g., re-meandering, physical habitat enhancement, riparian vegetation improvement) often do not lead to significant changes in the benthic invertebrate community, although positive effects on the availability and diversity of benthic habitats can be observed (Feld et al. 2011, Haase et al. 2013, Jähnig et al. 2009, Palmer et al. 2010). Among the most commonly assumed reasons for poor biological recovery of morphological restorations is the lack of nearby source populations capable of (re-)colonising a restored section (Feld et al. 2011, Sundermann et al. 2011b).

Dispersal is the central ecological mechanism that determines recolonisation (Hanski 1998), besides other important factors, for example, mating behaviour, oviposition and “propagule pressure” (Masters et al. 2007). Smith et al. (2015) showed that species composition models based on local habitat parameters can be improved by adding dispersal parameters. Yet, the knowledge on benthic invertebrate recolonisation and its environmental predictors is scarce. Dispersal capabilities largely differ among species (Elliott 2003). Merolimnic insect species (with winged adult stages) can cross catchments within a short time span, whereas dispersal of hololimnic species is limited to the wetted part of a water body. Even within merolimnic insects, there is a broad range of terrestrial dispersal

capabilities depending on the order considered (Bilton et al. 2001, Bis & Usseglio-Polatera 2004, Poff et al. 2006, Schmidt-Kloiber & Hering 2012, Vieira et al. 2006). Long distance dispersal events (> 50 km) have been reported for the dragonfly *Anax junius* (Wikelski et al. 2006) (order Odonata) and for passive (wind-assisted) dispersal of weak flyers (e.g., species of the insect orders Ephemeroptera, Diptera and Plecoptera) (Bilton et al. 2001), while short dispersal distances (< 5 km) have been found for *Hydropsyche hageni* (Kovats et al. 1996) (order Trichoptera).

As studies on landscape permeability have shown, dispersal further depends on the presence and type of landscape barriers (Keller et al. 2012, Pflüger & Balkenhol 2014). Clearly, weirs can fully block the upstream dispersal of larval stages. Therefore, dispersal barriers can hinder or even completely inhibit biological recovery after morphological restoration. However, the role of terrestrial structures is not easy to identify; they can either facilitate (e.g., Ehlert 2009) or hinder dispersal of adult stages (e.g., Blakely et al. 2006, Briers et al. 2002, Winterbourn et al. 2007).

In an earlier study, we found that considering physical dispersal barriers can improve prediction of dispersal over more conservative methods that, for instance, only use distance to estimate the recolonisation of a site (Sondermann et al. 2015). After analysing the distances to source populations, Sundermann et al. (2011a) found that the ecological quality of benthic communities was positively correlated with the presence of high-quality taxa within 5 km of a given site, which is in line with distances that have been found for fish in lower mountainous rivers of Germany (Stoll et al. 2013). Although they provide a useful rule of thumb, purely distance-based approaches neglect the role of riverine and landscape barriers in dispersal.

Here, we apply a new modelling approach, considering both species dispersal distances and landscape barriers. We combine the potential dispersal modes of merolimnic taxa and identified river sections, reachable either by larval aquatic up- and downstream dispersal or adult aerial dispersal. We chose a catchment with many restored river sections that has been depleted of habitat sensitive species for decades. This catchment offers ideal conditions for validation purposes because predictions can be validated against species presences and absences. The direction of recolonisation is evident. Species recently recorded in restored

river sections should theoretically be the offspring of surrounding source populations. Conversely, absences could be due to dispersal limitations.

Our study aims to predict the potential dispersal of the taxa based on (1) their present distribution patterns (2) their life stage dispersal capacities as documented in the literature or estimated by expert knowledge and (3) the potential barrier effects of different riverine and landscape structures. Therefore, we model the dispersal of 18 habitat-sensitive merolimnic taxa using a “least-cost” approach that has been frequently used for terrestrial (Adriaensen et al. 2003, Driezen et al. 2007, Koch & Smith 2008, Trénel et al. 2008) and aquatic organisms (Dedecker et al. 2007, Keller & Holderegger 2013). However, in contrast to Dedecker et al. (2007) and Keller & Holderegger (2013), we initially restrict the “least-cost” dispersal models to maximum dispersal distances, recorded or expected for each taxon, and then correct (reduce) the distances, if dispersal barriers are present. This new approach is contrasted with a “conservative” modelling approach based on the “5 km rule of thumb” as mentioned above, thus neglecting taxon-specific dispersal distances and barriers. We hypothesise that the inclusion of taxon-specific dispersal distances and barriers results in more precise models of dispersal and recolonisation.

3.2. Methods

3.2.1. Study area and data source

The study focuses on the Boye catchment (Federal State of North Rhine-Westphalia, Germany), which is a small lowland catchment (80 km^2) within the Emscher catchment, a tributary to the River Rhine. About 20 streams constitute a network of 90 km in length at altitudes ranging from 69 to 88 m a.s.l. (Figure 7). The floodplains are primarily used for residential, industrial and agricultural purposes.

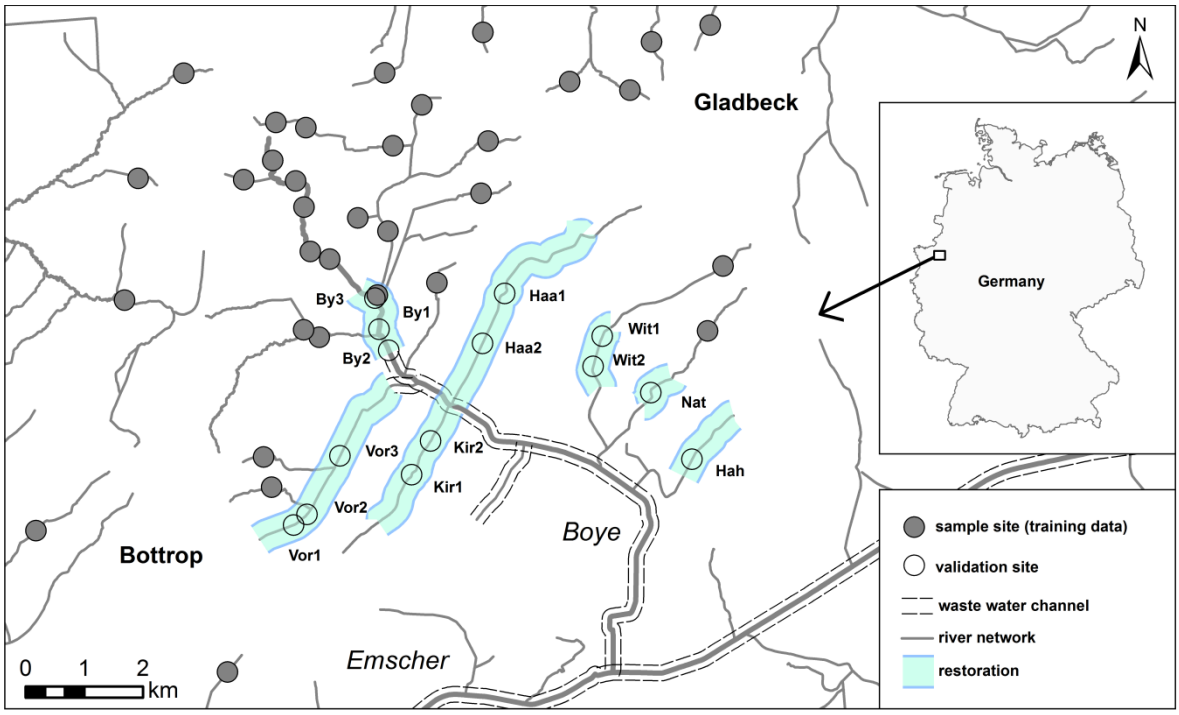

Figure 7: Study area and the location of 47 sample sites (Winking et al. 2013, Winking et al. 2014, Winking et al. unpublished). Species records at 33 sample sites were used to train dispersal models, while records from 14 sites (e.g., Haa1, Haa2) within restored river sections were used for model validation.

Until recently, many streams within the catchment were heavily channelised to transport untreated sewage from residential and industrial sources to the main water treatment plant further downstream (MKULNV-NRW 2014). Because of this severe degradation of river morphology and water quality, aquatic invertebrates could not establish populations except Oligochaeta (Winking et al. 2016). Between 1993 and 2012, seven stream sections were restored by separating wastewater transport from these streams, removing concrete bank enforcements and improving the riparian vegetation (Winking et al. 2013). This led to more natural cross-section profiles and improved water quality in seven streams.

Benthic invertebrate records were sampled at 47 sites within the model catchment during a field campaign in 2012 (Winking et al. 2013, Winking et al. 2014, Winking et al. unpublished). Sample units were stratified by substrate type (stones, pebbles, organic matter, etc.) that occurred within the sample site. Thirty-three sample sites were located in non-restored river sections. These sites were used as training data. The remaining 14 sites were located in restored sections and provided the validation data, referred to as validation sites hereafter (Figure 7).

We developed dispersal models for 18 aquatic invertebrate taxa (Table 8) that are present in the study area and are sensitive to habitat degradation (Winking et al. 2014). The taxa cover various insect orders (Odonata, Plecoptera, Trichoptera, Coleoptera and Diptera). Additionally, an inventory of potential in-stream and terrestrial dispersal barriers was performed. These barriers were derived from detailed spatial maps (Table 9) and were stored in separate maps (GIS raster format, spatial resolution = 5 × 5 m).

Table 8: Maximum dispersal distances (m) per dispersal mechanism and lifecycle applied in this study for model taxa (n = 18), estimated by the authors. Estimation was based on the literature, marked by footnotes.

	Order	Taxon / Taxa group	Aerial (m)	Aquatic upstream (m)	Aquatic downstream (m)
strong dispersers	Trichoptera	*Glyphotaelius pellucidus*	4,000[a, b, c, d, e]	100[a, f]	200[a]
		Halesus radiatus			
		Micropterna lateralis/sequax			
		Micropterna nycterobia			
		Potamophylax nigricornis			
		Potamophylax sp.			
		Plectrocnemia conspersa conspersa	4,000[a, c, e]	50[a]	100[a]
	Odonata	*Cordulegaster boltonii*	4,000[a, g, h, i, j]	30[a, i]	50[a, i]
weak dispersers	Trichoptera	*Sericostoma flavicorne/personatum*	1,400[a, c, d, k]	30[a, l, m]	50[a, n]
		Odontocerum albicorne	1,000[a, i]	50[a, l, m]	100[a, i]
		Lithax obscurus	1,000[a, c, i]	50[a, i]	50[a, i]
	Coleoptera	*Elodes minuta*-group	1,000[a]	30[a]	50[a]
	Trichoptera	*Lype reducta*	800[a, c, i]	30[a, i]	50[a, i]
	Diptera	*Atherix/Ibisia* sp.	800[a, i]	30[a, i]	50[a, i]
		Chelifera sp.	800[a, i, o]	30[a, i]	50[a, i, o]
		Hemerodromia sp.			
	Plecoptera	*Amphinemura* sp.	500[a, c, i, p, q]	200[f, i]	300[f, i]
		Nemoura cinerea cinerea			

[a] = Bis & Usseglio-Polatera (2004), [b] = Malicky (1987), [c] = Schmidt-Kloiber & Hering (2012), [d] = Sode & Wiberg-Larsen (1993), [e] = UBA (2014), [f] = Elliott (2003), [g] = Buchwald (2003), [h] = Conze et al. (2011), [i] = Poff et al. (2006), [j] = Vieira et al. (2006), [k] = Masters et al. (2007), [l] = Elliott (1971), [m] = Rawer-Jost et al. (1999), [n] = Jackson et al. (1999), [o] = Carvalho & Uieda (2006), [p] = Mendl & Müller (1974), [q] = Zwick (1990).

Table 9: Data sources used to identify and parameterise dispersal barriers.

	Potential barriers	Data source	Reference
Aerial and aquatic dispersal	Deciduous forest Coniferous and mixed forest Open land Urban area Water body Impounded water bodies	Land use map ("ATKIS basic DLM 2007")	Afflerbach & Kunze (2006)
	Riparian vegetation (composition) Presence of culverts	Physical habitat survey map	MUNLV-NRW (2003)
Aquatic dispersal	Presence of weirs/groundsills, relevant as migration barriers	Map of transverse structures ("Querbauwerke-Informationssystem NRW")	Anderer et al. (2007)
	Rivers, loaded continuously with untreated urban wastewater	Map of river network	Emschergenossenschaft (unpublished data)

3.2.2. Predicting recolonisation

We predicted the dispersal and potential recolonisation of river sites for each taxon separately, based on the source populations within the 33 non-restored sites (training data) using a "least-cost" modelling approach (Adriaensen et al. 2003, Dedecker et al. 2007, Sondermann et al. 2015). This method is based on a least-cost algorithm, which combines the spatial distribution of a taxon's source population, the maximum dispersal distance for each life cycle (Table 8) and landscape resistance for dispersal, hereafter parameterised with the cost of dispersal barrier friction (see Appendix: Table A2, Table A3). This barrier friction was expressed as costs per meter, with higher costs for landscape elements that hinder dispersal (e.g., weirs for aquatic upstream dispersal) and lower costs for landscape elements that facilitate dispersal (see Table A3). In our approach we parameterised landscape elements that facilitate dispersal with a cost value of 1 per meter. To restrict the prediction of dispersal range to a maximum dispersal distance (e.g., aerial dispersal of *Halesus radiatus* = 4,000 m), we translated the maximum dispersal distance into a maximum accumulated dispersal cost value (i.e., 4,000 for aerial dispersal of *H. radiatus*). Therefore, without dispersal barriers (cost value per meter = 1), the predicted least-cost dispersal range would extend to 4,000 m from a given source population of *H. radiatus*. In the presence of dispersal barriers (cost value per meter > 1), the accumulated dispersal costs exceed the maximum accumulated dispersal cost value earlier, i.e., the predicted

dispersal range is lower than 4,000 m. Further mathematical details on the least-cost algorithm are given in ESRI (2011a). The least-cost algorithm was applied by using the tools *Cost Distance* (ESRI 2011a) and *Path Distance* (ESRI 2011b) that are part of the Spatial Analyst extension of ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). *Cost Distance* allowed us to describe the potentially undirected aerial dispersal of adult aquatic insects, while we used *Path Distance* to deal with the directed aquatic upstream and downstream dispersal of larval stages. *Path Distance* requires data on the flow directions within the river network which were derived by coding river segments continuously from source to mouth, and further processing the segmented network using the ArcGIS tool *Flow Direction* (ESRI 2011c). These first steps resulted in a map for each of the 18 model taxa, showing the potential dispersal range through aerial, aquatic upstream and aquatic downstream dispersal within one life-cycle. Second, the information on dispersal range was reduced to the Boye river network for each taxon and further combined for all taxa by the ArcGIS tool *Combine* (ESRI 2011d). This merged map contains the qualitative and quantitative information for each river site, including which and how many taxa are predicted to be capable of dispersing to this site. Predictions are made at high resolution, resulting in a total of 35,338 sections for the entire network, referred to as spatial units “SUs” hereafter. Hence, for each SU, the presence of between 0 and 18 taxa is predicted.

The predictions are compared with predicted taxon presences based on a conservative approach, to test if source populations within a 5 km radius (Sundermann et al. 2011a) around restored sites can be reliable predictors of recolonisation. This distance was chosen and tested, because this distance could be used as a rule of thumb in dispersal modelling according to recent research of Sundermann et al. (2011a) and Stoll et al. (2013). Therefore, 5 km buffers were generated for each of the 33 non-restored sites (training data) using ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). Recolonisation was assumed if an SU or restored section was located within a buffer.

3.2.3. Model validation

The predictions of both the least-cost and conservative modelling approaches were validated at 14 sites. We compared the actual number of taxa at the

validation sites to the predicted number of taxa from the conservative and least-cost dispersal modelling results. Wilcoxon's signed rank test with Bonferroni correction was applied using R (R Core Team 2014) to test the predicted number of taxa against the actual number of taxa at the validation sites.

The correct classification rate (CCR), sensitivity and specificity were chosen as the parameters to validate the dispersal predictions at each validation site. The CCR relates the number of correctly predicted presence and absence points of taxa to the total number of predictions at each validation site. Sensitivity relates the correct predictions of presences to the overall number of actual presences. Specificity relates the correct predictions of absences to the overall number of actual absences. All parameters were derived from elements of the confusion matrix (Fielding & Bell 1997) by comparing the predicted reachability/non-reachability (presence/absence) with the observed presence/absence at the validation sites (n = 14). The validation parameters for the least-cost (LC) and conservative (CON) models were compared using Wilcoxon's signed rank test (Statistica 10, StatSoft). This procedure addresses each validation site separately and assesses the predictive power across all modelled taxa. In addition, CCR was calculated for each taxon separately across all validation sites, to compare the taxon-specific predictive power of least-cost and conservative models.

3.3. Results

3.3.1. Comparison of dispersal models

The conservative approach resulted in a significantly higher potential for recolonisation compared to the LC approach, as exemplarily shown for *H. radiatus* (Figure 8) and across all taxa (Figure 9).

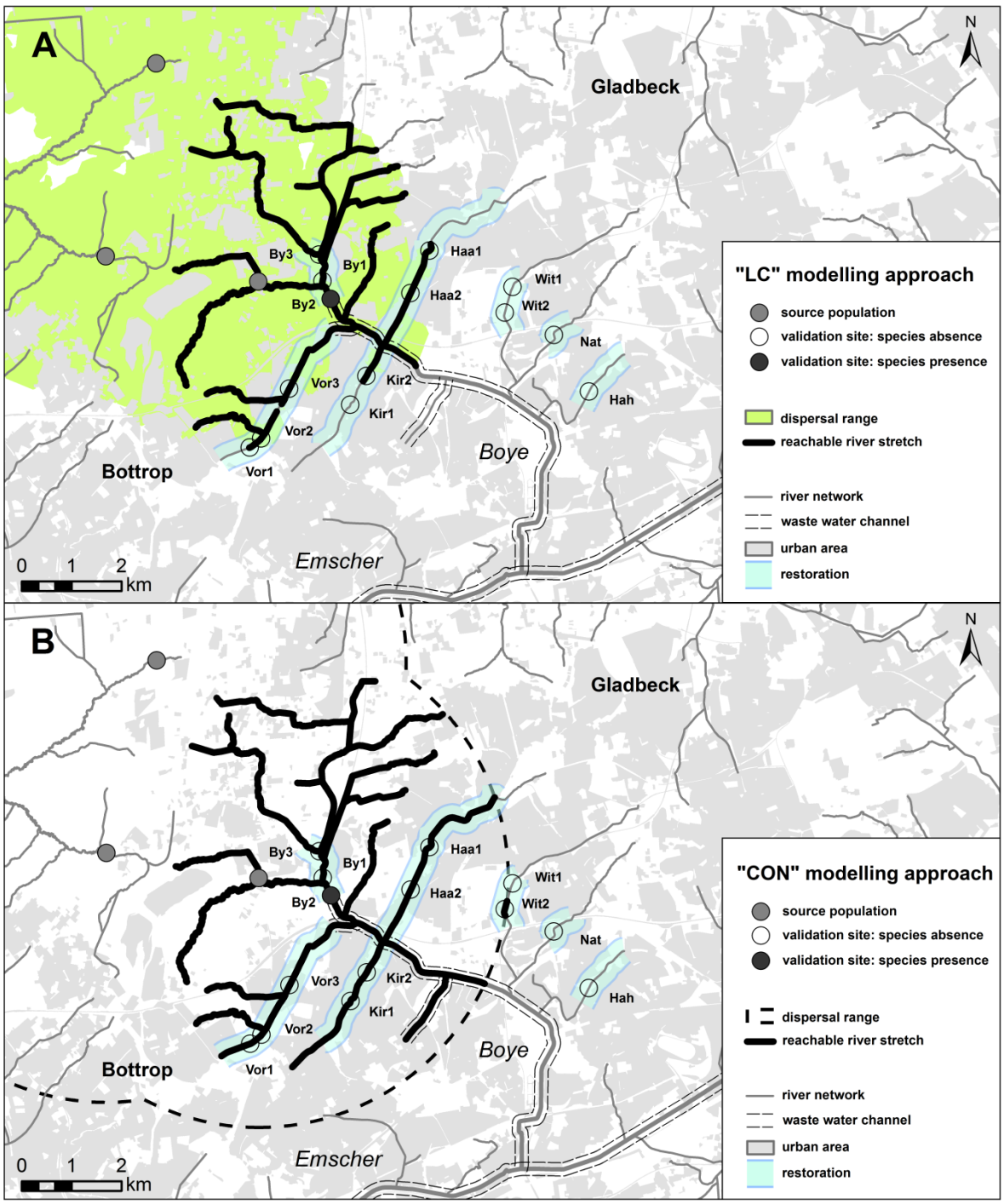

Figure 8: Prediction of the dispersal range of *Halesus radiatus* (order: Trichoptera) from least-cost ("LC", Fig. A) and conservative modelling ("CON", Fig. B) to illustrate the outcomes of different dispersal modelling approaches. Additionally, given source populations of *H. radiatus* within the study area and actual records within the validation sites are shown.

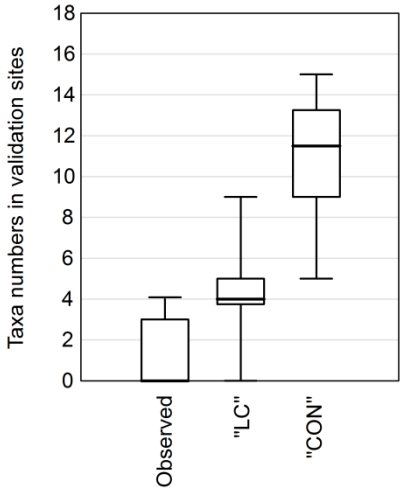

Figure 9: The observed number of modelled taxa at the validation sites compared to the predicted number of taxa; “LC” = least-cost modelling approach, “CON” = conservative approach; the median is represented by the horizontal line.

Validation sites (= restored sites) were predicted to be recolonised by five to 15 taxa, based on the conservative model, while only a maximum of nine taxa resulted from the LC model. Wilcoxon’s signed rank test with Bonferroni correction reveals significant differences ($p < 0.01$) in the number of taxa between all groups: “actual” vs. “least-cost”; “actual” versus “conservative”; “least-cost” versus “conservative”. Additionally, the conservative and the LC approach resulted in a strong geographical pattern, with a higher recolonisation potential in the north-western part of the Boye catchment and a lower potential in the south-eastern tributaries (Figure 10).

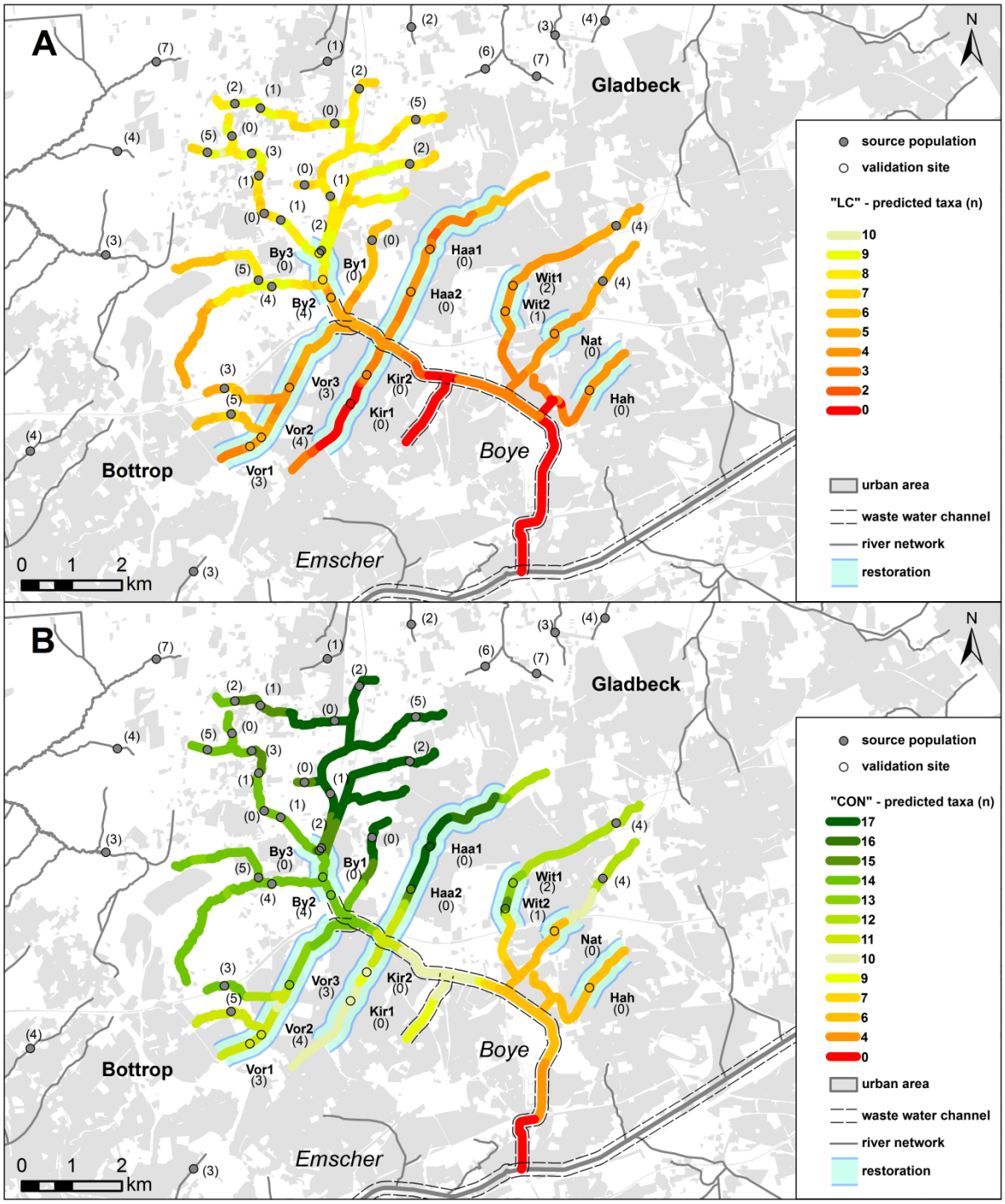

Figure 10: Differently coloured river network indicates the predicted number of taxa (max. 18 taxa), based on least-cost ("LC", Fig. A) and conservative modelling approaches ("CON", Fig. B). The actually observed number of taxa is indicated for each sample site in brackets.

3.3.2. Validation of dispersal models

At best, both dispersal models reveal only moderate model fits. Site-specific LC predictions of the 18 model taxa result in CCRs > 70% for 11 out of the 14 sites (= 71%). Equally high CCRs were achieved for only 2 out of the 14 sites based on the conservative approach (= 14%). The CCR and specificity were better for the least-cost models and differed significantly from the conservative approach (Figure 11). On average, the CCR was 37% points higher ($p < 0.01$) and specificity was 42% points higher for the least-cost approach ($p < 0.01$) (Table 10). Sensitivity was 18% points higher for the conservative approach, but sensitivity was comparable between both approaches (Figure 11; significance was not determined due to small sample size). However, both the least-cost and conservative predictions did not match the actual number of taxa encountered in the field. Both approaches tended to overestimate the actual occurrences. This overestimation was more pronounced in the results of the conservative approach (Figure 9).

Considering all taxa (Table 11), a high predictive power (CCR = 100%) is found for eight out of 18 taxa (= 44%) with least-cost modelling. No taxon achieved this high a CCR with the conservative approach.

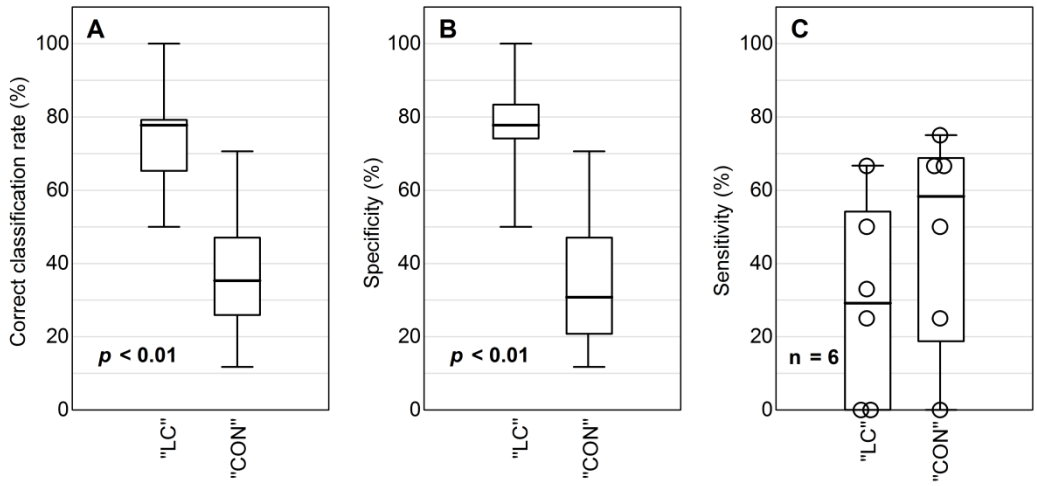

Figure 11: Correct classification rate (A), specificity (B), and sensitivity (C) of dispersal models for all validation sites (n = 14) and the least-cost ("LC") and conservative ("CON") modelling approach; for sensitivity, original values (see Table 10) were plotted as circles, without testing for significant differences because of low sample size (n = 6).

Table 10: Validation of dispersal models per site and the conservative ("CON") and least-cost ("LC") modelling approach, based on correct classification rate (CCR), sensitivity (= actual presences that are correctly predicted as such), specificity (= actual absences that are correctly predicted as such) and difference (∆-% points) between modelling approaches.

Site ID	"CON" CCR (%)	"CON" sensitivity (%)[a]	"CON" specificity (%)	"LC" CCR (%)	"LC" sensitivity (%)[a]	"LC" specificity (%)	∆ CCR (% points)	∆ sensitivity (% points)[a]	∆ specificity (% points)
By1	29	n.a.	29	56	n.a.	56	+ 26	n.a.	+ 26
By2	41	75	31	78	50	86	+ 37	− 25	+ 55
By3	24	n.a.	24	50	n.a.	50	+ 26	n.a.	+ 26
Haa1	12	n.a.	12	83	n.a.	83	+ 72	n.a.	+ 72
Haa2	12	n.a.	12	78	n.a.	78	+ 66	n.a.	+ 66
Vor1	47	67	43	78	67	80	+ 31	0	+ 37
Vor2	29	25	31	61	25	71	+ 32	0	+ 41
Vor3	41	67	36	72	33	80	+ 31	− 33	+ 44
Kir1	47	n.a.	47	100	n.a.	100	+ 53	n.a.	+ 53
Kir2	47	n.a.	47	83	n.a.	83	+ 36	n.a.	+ 36
Wit1	29	50	27	67	0	75	+ 37	− 50	+ 48
Wit2	12	0	13	72	0	76	+ 60	0	+ 64
Nat	71	n.a.	71	78	n.a.	78	+ 7	n.a.	+ 7
Hah	71	n.a.	71	78	n.a.	78	+ 7	n.a.	+ 7
					Arithmetic mean=		+ 37	− 18	+ 42

[a] n.a. = no observed presences in validation sites to calculate the parameter "sensitivity".

Table 11: Correct classification rate (CCR) of least-cost (LC) and conservative (CON) models for modelled taxa and their prevalence in the study area.

Taxon	**Prevalence beyond validation site (n = 33)**	**Prevalence within validation sites (n = 14)**	**"LC" CCR (%)**	**"CON" CCR (%)**
Chelifera sp.	4	0	100	21
Lype reducta	3	0	100	14
Amphinemura sp.	2	0	100	57
Sericostoma flavicorne/personatum	1	0	100	71
Odontocerum albicorne	1	0	100	21
Lithax obscurus	1	0	100	71
Atherix/Ibisia sp.	1	0	100	86
Hemerodromia sp.	1	0	100	50
Potamophylax nigricornis	1	1	93	57
Cordulegaster boltonii	5	0	71	14
Potamophylax sp.	3	2	71	43
Elodes minuta-group	20	2	57	14
Micropterna nycterobia	2	0	57	36
Nemoura cinerea cinerea	18	6	50	57
Halesus radiatus	3	1	43	29
Plectrocnemia conspersa conspersa	12	0	36	0
Glyphotaelius pellucidus	9	3	29	21
Micropterna lateralis/sequax	8	2	21	14

3.4. Discussion

3.4.1. A unique opportunity to reduce the distribution-related uncertainty

The combination of the known distribution of refugia, together with the knowledge of the parts of the Boye system that were free of benthic invertebrates before revitalisation opened an unprecedented option to study the recolonisation of the system. Any taxon found at a formerly polluted site must have recolonised the site starting from one of the known refugia. It is this peculiarity of the Boye system that allowed us to develop the least-cost dispersal models and to compare our results with those of a purely distance-based (conservative) approach following the findings of Sundermann et al. (2011a) and Stoll et al. (2013).

Dispersal models are based on the distribution of the targeted taxa, i.e. the presence and absence of each taxon needs to be known for a sufficient number of sites within the model area. Hence, the approach is prone to false negatives (i.e., overlooked taxa). With the aforementioned peculiarity of our study area, we were able to significantly reduce this uncertainty.

3.4.2. Comparison of least-cost and distance-based model results

Overall, least-cost (LC) dispersal models are only of moderate strength, which is most likely connected to the input parameters that neglect important but unconsidered predictors as mentioned below. Nevertheless, irrespective of the model goodness of fit, predictions of presences and absences are reliable and can help restoration practitioners make decisions about where to restore (e.g., close to sources not disconnected by barriers).

These predictions tend to be better for LC dispersal models in terms of two out of three of the validation parameters (CCR and specificity), which in particular is true for correctly predicted absences. Higher correctly predicted absences are likely to be linked to barriers, which remain unaddressed in the purely distance-based conservative approach. Both approaches tend to overestimate the actual number of taxa, again with the LC models performing better. This may be linked to ongoing succession in the benthic invertebrate community (Winking et al. 2016) leading to the conclusion that predicted presences of invertebrate assemblages might be fulfilled in the near future. Another reason may be specific habitat conditions that are not provided in the early years after restoration. A high predictive power (CCR = 100%) was found for eight out of the 18 taxa (Table 11). These eight taxa can be characterised as taxa with low dispersal capabilities (< 1,500 m, Table 8). Therefore, one may conclude that the predictive power is generally high for “weak” dispersers, but the prevalence of these taxa is low (Table 11). Additionally, four of these taxa are adapted to crenal habitats (*Chelifera* sp., *Odontocerum albicorne* and *Lithax obscurus*). This leads to the point that the low prevalence and recolonisation may be a result of unsuitable local habitat parameters rather than dispersal constraints. The low prevalence leads to a validation data set upon taxa

absences, which are of lower confidence than taxa presences as false negative records can be due to sampling method and sampling effort. Therefore, the observed high predictive power for “weak” dispersers must be considered as a subject to uncertainty.

The lowest predictive power with least-cost modelling is revealed for *Halesus radiatus, Glyphotaelius pellucidus*, *Plectrocnemia conspersa conspersa* and *Micropterna lateralis/sequax* (Table 11). *Halesus radiatus* is specialised to particular organic matter and dead wood (Schmidt-Kloiber & Hering 2012). *Glyphotaelius pellucidus* is adapted to lentic sections (Speth & Brinkmann 1998) and coarse particular organic matter (Schmidt-Kloiber & Hering 2012). Both species require organic microhabitats. These microhabitats may be lacking in “younger” restoration sites, where riparian vegetation is not fully established (Winking et al. 2014). For these two species, habitat constraints may limit the predictive power of least-cost modelling. One may conclude that constraining dispersal modelling to habitat generalists may improve the predictive power. However, if habitat specialists (e.g., *H. radiatus* and *G. pellucidus*) are excluded from dispersal modelling, we do not achieve a significant overall improvement (CCR < + 5%). *Plectrocnemia conspersa conspersa* and *Micropterna lateralis/sequax* do not depend on organic microhabitats. This is reflected by their more widespread occurrence at non-restored sites within the Boye catchment. For these species, habitat constraints may not be the limiting factor for colonisation. More likely, the parametrisation of the dispersal models might be incorrect, e.g., overestimated dispersal distances or underestimated barrier effects on dispersal.

Therefore, the difference between actual and predicted recolonisation may be due to numerous reasons (e.g., lack of habitats in restored sites, overestimated maximal dispersal distance or underestimated dispersal barriers). Yet, considering dispersal barriers and taxon-specific dispersal distances may be essential to predicting recolonisation of restored river sites.

4. Summary, conclusion and future prospects

4.1. Summary

Worldwide, many lotic ecosystems are heavily impacted by anthropogenic disturbance, leading to a significant decline in freshwater biodiversity. In recent years, increasing efforts have been directed towards the restoration and revitalisation of disturbed streams and rivers to reverse this trend. Although it is widely acknowledged that species dispersal is the key to the recolonisation of restored streams and rivers and ultimately to their ecological recovery, dispersal often remains unaddressed in restoration ecology.

For this reason, the present thesis had two main objectives:

1) The development and application of a dispersal modelling approach that considers taxon-specific dispersal distances and dispersal barriers.
2) The validation and comparison of this dispersal modelling approach, based on taxon-specific dispersal distances and barriers, against a purely distance-based approach.

Therefore, this thesis is divided into two main chapters dealing with these objectives. Following this structure, background information and main results are summarised in the next paragraphs for each chapter.

Chapter 2: Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment

In chapter 2, we present an approach to predict larval (aquatic) and adult (terrestrial) dispersal ranges of three lotic insect species (*Hydropsyche dinarica* [Trichoptera], *Calopteryx virgo* [Odonata] and *Dinocras cephalotes* [Plecoptera]) within one life cycle. The actual species' distributions (presence / absence) were obtained from a total of 1,198 sites evenly distributed within the Ruhr catchment, North Rhine-Westphalia, Germany. The predictions for aquatic and terrestrial dispersal were made for two scenarios: with and without dispersal barriers included in the predictive modelling. In-stream dispersal barriers included weirs,

dams, culverts and impounded water bodies, whereas terrestrial barriers were related to the stream corridor (degraded riparian vegetation) and different forms of land use (urban land use, coniferous and deciduous or mixed forest, open land, road infrastructure). We applied a “least-cost” modelling approach and combined each species’ life-cycle-specific dispersal capabilities and the corresponding dispersal barrier’s “friction” costs in a grid-based GIS model.

Among the three model species, *H. dinarica* was the best disperser and was predicted to be able to reach between 81% (without barriers) and 67% (with barriers) of all river sections in the model catchment within one life cycle. Aerial (terrestrial) dispersal was by far the most important dispersal mechanism. For validation purposes, we conducted a logistic regression analysis to identify sample sites with environmentally suitable habitats. Within these sites that are not considered constrained by habitat limitations, the comparison of actual and predicted absences revealed a better match, if barriers were included in the dispersal models. At the same time the mismatch of actual absences and predicted presences decreased. Our results suggest that dispersal models can contribute to a better assessment of the potential recolonisation of rivers. Yet, the dispersal of lotic insects may be considerably overestimated if dispersal barriers remain unaddressed.

Chapter 3: Application and validation of a new approach for modelling benthic invertebrate dispersal: first colonisation of a former open sewer system

Within a heavily modified catchment, formerly polluted streams are now free of untreated wastewater. Additionally, the morphology of streams has been improved by physical habitat restoration. Both water quality and structural improvements offered a unique opportunity to investigate the recolonisation of restored sections by benthic invertebrates. As dispersal is a key mechanism for recolonisation, we developed a method to predict the dispersal of 18 aquatic insect taxa to 35,338 river sections (section length: 2 m) within the catchment. Source populations of insect taxa were sampled at 33 sites. In addition, 14 morphologically restored sites were sampled and constituted the validation dataset. As in chapter 2, we applied a “least-cost” modelling approach within a raster-based GIS model, combining

taxon-specific aquatic and terrestrial dispersal capabilities with the “friction” that physical migration barriers impose on dispersal of aquatic and terrestrial stages. This taxon-specific modelling approach was compared to a conservative modelling approach, assuming a Euclidean distance of 5 km, based on a former study, as the maximum dispersal distance for any source population regardless of dispersal barriers.

Least-cost modelling showed a significantly better performance in terms of the correct classification rate (CCR) and true predicted absences (specificity), with on average 37% points higher CCR and 42% points higher specificity. Sensitivity was 18% points lower. At 71% of the validation sites, recolonisation was predicted with at least a modest goodness of fit (CCR > 70%). Conversely, the conservative modelling approach achieved a modest goodness of fit for only 14% of the validation sites. For 44% of the taxa, least-cost modelling showed a high CCR (= 100%), whereas the conservative approach showed a high CCR for none of the taxa. Our approach can help water managers select appropriate sites for restoration to increase recolonisation and biological recovery.

4.2. Conclusion and future prospects

The results of the present thesis, summarised in the previous chapter, are expected to improve the understanding of benthic invertebrate’s dispersal and (re-)colonisation within and between rivers. In the following paragraphs, main conclusions and methodological limitations are discussed and suggestions for future research will be made. As the present thesis is structured in two main chapters, the conclusions will be made separately for each main chapter. Finally, new insights on species’ dispersal and species’ distribution, given from other studies with co-authorship of this author, will be summarised.

Chapter 2: Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment.

Modelling the dispersal of merolimnic aquatic insects requires reliable data on source populations of species and their dispersal capabilities, ideally addressing

all relevant stages of the species' life cycle. Furthermore, it is crucial to know the presence and implications of in-stream and terrestrial landscape structures that may act as dispersal barriers and significantly reduce or hinder dispersal.

The amount of reachable river stretches varies between species and can inform restoration management about those river stretches that are reachable by a high number of target species. This, however, would require to establish dispersal models for all species of interest. In the case of aquatic insects, terrestrial (aerial) dispersal of winged life cycle stages is much more effective than aquatic dispersal of larval stages. Consequently, dispersal is more affected by the presence of landscape barriers (e.g., urban areas, dense coniferous forests) than it is by the presence of in-stream barriers (e.g., weirs). However, the establishment of populations is more complex, as it requires not only suitable habitat conditions in the target reach but also the arrival of many individuals, which might be more likely with aquatic dispersal.

In summary, our results underline the importance of landscape barriers for dispersal modelling. Without considering barriers, the models tended to overestimate dispersal more than models "with barriers". However, we conclude that dispersal modelling continues to be subject to uncertainty as long as species- and life cycle stage-specific dispersal distances are based rather on expert knowledge than on empirical data. The same applies to the friction costs that landscape and in-stream barriers may impose upon dispersal. Future studies should fill these knowledge gaps, for instance, by experimentally analysing dispersal distances in different landscape elements and by linking dispersal models to population genetics.

Chapter 3: Application and validation of a new approach for modelling benthic invertebrate dispersal: first colonisation of a former open sewer system.

Compared to the purely distance-based prediction of dispersal and recolonisation, the integration of taxon-specific dispersal capabilities and dispersal barriers improved the predictive power of dispersal models. Both the correctly predicted presences and absences (correct classification rate) and absences (specificity) were higher with our model approach. The validation results, although modest,

indicate that dispersal limitations are decisive parameters that determine actual taxa distribution. Yet, the establishment of populations after recolonisation is beyond the scope of this study, as it requires the arrival of many individuals and repeated quantitative field sampling over several recolonisation cycles of the targeted taxa.

However, despite of the beneficial situation in the model area, with known source populations and a low probability of false negative taxon records, we were not able to reliably predict the actual presence and absence of taxa within the Boye system. Future studies should address three important aspects: i) reliable dispersal capabilities (distances per time unit) are required, which might be derived from mark-and-recapture studies; ii) landscape friction costs potentially imposed by in-stream and terrestrial barrier structures need to be recorded and parameterised; iii) repeated samples of the same sites over several years need to be analysed with regard to habitat suitability and population size of the targeted taxa, to be able to address actual recolonisation after dispersal.

Additional contributions to other research

Besides preparing the present thesis, the author contributed to Elbrecht et al. (2012), Gies et al. (2015a), Gies et al. (2015b), Schröder (2015) and Schröder et al. (2015). In summary, these studies show that actual species distribution is the result of a plenty of factors and species' dispersal and (re-)colonisation are processes with a high degree in complexity that can only be predicted with strongly simplifying models.

Elbrecht et al. (2012) analysed genetic material of *Dinocras cephalotes* (Plecoptera), collected for the present thesis, and found that gene flow between most populations within the Ruhr-System is evident. Therefore, one can conclude that dispersal barriers and dispersal distances of this weak flying species are of less importance in the long term (> decades). Nevertheless, in a short term (< 10 years) they are presumably fundamental to predict dispersal and the recolonisation of local restorations. In Schröder (2015) the author contributed to the development of "least-cost" dispersal models for 10 benthic invertebrates that there coupled with species habitat models to predict the recolonisation potential. The results showed that both, dispersal models and habitat models are subject to

uncertainty as predictions depend highly on the quality of the input data (e.g., maximum dispersal distances).

In Schröder et al. (2015) it was evident that species composition and species occurrence can be influenced by a single environmental parameter (here: salinity). The study of Gies et al. (2015a) is based on 225 river sites, sampled by the authors. In this study, the actual distribution of eleven benthic invertebrate species was compared to the predicted distribution based on species habitat models instead of species dispersal models. The results showed that validation approaches can be improved by separate field data on actual species occurrence that was not used for development of species habitat models before. In Gies et al. (2015b) the prediction of species distribution was based on species habitat models dealing with broadscale environmental parameters. The results showed that predictions of species distribution based on broadscale environmental parameters are only suited for single benthic invertebrate species. Furthermore, transferability of species habitat models between catchments was low, presumably because of different environmental conditions and ongoing effects of former land use.

5. Zusammenfassung, Schlussfolgerungen und Ausblick

5.1. Zusammenfassung

Weltweit sind Fließgewässersysteme von anthropogenen Überprägungen betroffen, was zu einer bedeutenden Abnahme der Biodiversität in Bächen und Flüssen geführt hat. Um diesen Trend umzukehren, sind in der Vergangenheit vielfache Anstrengungen in die Renaturierung betroffener Gewässer gelenkt worden. Doch obwohl die Ausbreitungsfähigkeit benthischer Gewässerorganismen ein Schlüssel zur Wiederbesiedlung renaturierter Gewässer ist, wurde diesem Faktor in bisherigen Studien oft wenig Beachtung geschenkt.

Aus diesem Grund ergab sich für die vorliegende Dissertation folgende Zielsetzung:

1) Die Entwicklung und Anwendung von Ausbreitungsmodellen, mit denen taxon-spezifische Ausbreitungsdistanzen und -barrieren berücksichtigt werden können.
2) Die Validierung und ein Vergleich dieser Ausbreitungsmodelle mit einfacheren Ausbreitungsmodellen, die alleine Ausbreitungsdistanzen berücksichtigen.

Diese Ziele werden in den zwei Hauptkapiteln (Kapitel 2 und Kapitel 3) behandelt. Dieser Struktur folgend werden im Folgenden die wesentlichen Ergebnisse für jedes Kapitel separat zusammengefasst.

Kapitel 2: Modellierung des Effekts aquatischer und terrestrischer Barrieren auf die Ausbreitung aquatischer Insektenarten: eine Fallstudie aus einem mitteleuropäischen Gewässereinzugsgebiet im Mittelgebirge.

Im zweiten Kapitel wird für drei verschiedene merolimnische Insektenarten (*Hydropsyche dinarica* [Trichoptera], *Calopteryx virgo* [Odonata] und *Dinocras cephalotes* [Plecoptera]) ein Modellansatz zur Vorhersage der larvalen (aquatischen) und adulten (terrestrischen) Ausbreitungsreichweite innerhalb eines

Lebenszyklus vorgestellt. Die aktuelle räumliche Verteilung der Artvorkommen wurde mit insgesamt 1.198 gleichmäßig verteilten Probestellen innerhalb des Ruhreinzugsgebiets (Nordrhein-Westfalen) ermittelt und qualitativ (d. h. als Vorkommen / Nichtvorkommen) beschrieben. Die Vorhersagen zur aquatischen und terrestrischen Ausbreitung wurden für zwei Szenarien getroffen: zum einen mit Berücksichtigung und zum anderen ohne Berücksichtigung aquatischer und terrestrischer Ausbreitungsbarrieren. Wehre, Staudämme, Staubereiche und Gewässerverrohrungen wurden als aquatische Ausbreitungsbarrieren berücksichtigt. Als terrestrische Barrieren wurden unterschiedliche Landnutzungsformen (Siedlungsgebiete, Nadelwald, Laub- und Mischwald, Offenland, Straßen- und Wegenetz) sowie die Ausprägung des Gewässerkorridors (Naturnähe der Ufervegetation) berücksichtigt. Die Ausbreitungsmodelle beruhen auf einem „Least-Cost“-Ansatz, mit dem die art- und lebenszyklusspezifischen Ausbreitungsfähigkeiten mit dem spezifischen Widerstandswert einer Ausbreitungsbarriere (ausgedrückt in Kosten) in einem rasterbasierten GIS-Model kombiniert werden konnten.

Von den drei Insektenarten, wurde für *H. dinarica* die höchste Ausbreitungs-reichweite vorhergesagt: bei Berücksichtigung von Barrieren wird eine Erreichbarkeit von 67% aller Gewässerabschnitte im Einzugsgebiet innerhalb eines Lebenszyklus vorhergesagt gegenüber 81% aller Gewässerabschnitt bei Nichtberücksichtigung von Barrieren. Die terrestrische Ausbreitung im flugfähigen Stadium war der weit bedeutendste Ausbreitungsmechanismus für alle drei Arten. Zur Validierung der Vorhersagen wurde anhand verschiedener Umweltparameter eine logistische Regressionsanalyse durchgeführt um diejenigen Probestellen zu identifizieren, die geeignete Habitate für die untersuchten Insektenarten aufweisen. Für diese Stellen, deren Besiedlung nicht durch Habitatdefizite eingeschränkt ist, ergab ein Vergleich der aktuellen und vorhergesagten Nichtvorkommen eine bessere Übereinstimmung, wenn Barrieren in den Ausbreitungsmodellen berücksichtigt wurden. Außerdem nahm die Unstimmigkeit zwischen aktuellen Nichtvorkommen aber vorhergesagten Vorkommen ab. Insgesamt deuten die Ergebnisse darauf hin, dass Ausbreitungsmodelle zu einer besseren Einschätzung der potenziellen Wiederbesiedlung von Fließgewässern beitragen können. Ohne eine Berücksichtigung von Ausbreitungsbarrieren kann

die Ausbreitung und Wiederbesiedlung von Fließgewässerinsekten jedoch weit überschätzt werden.

Kapitel 3: Anwendung und Validierung eines neuen Ansatzes zur Modellierung der Ausbreitung benthischer Wirbelloser: erste Besiedlung eines zuvor offenen Abwassersystems.

Innerhalb eines erheblich veränderten Gewässernetzes, wurde an einzelnen Gewässern die ehemalige offene Abwasserführung in separate Abwasserkanäle überführt. Die zuvor verschmutzen Gewässer sind nun frei von unbehandeltem Abwasser. Zusätzlich wurden die hydromorphologischen Gewässereigenschaften durch strukturelle Renaturierungsmaßnahmen verbessert. Mit den Verbesserungen in stofflicher und gewässerstruktureller Hinsicht ergab sich eine einmalige Möglichkeit, die Wiederbesiedlung renaturierter Gewässerabschnitte durch merolimnische Gewässerinsekten zu untersuchen. Ein fundamentaler Mechanismus für die Wiederbesiedlung ist die Ausbreitung von Individuen. Es wurden daher Modelle für insgesamt 18 Gewässerinsekten entwickelt, mit der die Ausbreitung innerhalb von 35.338 Gewässerabschnitten (Abschnittslänge: 2 m) innerhalb des Gewässernetzes modelliert werden konnte. 33 Probestellen entlang der Gewässer dienten der Identifikation von Quellpopulationen für die Wiederbesiedlung. Zusätzlich dienten 14 Probestellen an den renaturierten Gewässerabschnitten als Datensatz zur Validierung der Vorhersagen. Wie in Kapitel 2 kam für die Vorhersagen ein Least-Cost-Ansatz innerhalb eines rasterbasierten GIS-Models zur Anwendung. Mit diesem Ansatz konnten taxonspezifische Ausbreitungsdistanzen mit dem Widerstand physischer Ausbreitungsbarrieren verknüpft werden kann. Dieser artspezifische Modellierungsansatz wurde anschließend verglichen mit einem konservativen Modellierungsansatz, bei dem, basierend auf eine frühere Studie, eine euklidische Ausbreitungsdistanz von 5 km angenommen wird. Ausbreitungsbarrieren sowie taxon- und lebenszyklusspezifische Unterschiede in der Ausbreitungsfähigkeit und bleiben in diesem konservativen Modellierungsansatz unberücksichtigt.

Die Least-Cost-Modellierung zeigte signifikant bessere Ergebnisse bei der „Rate korrekter Vorhersagen“ (CCR) und den richtig vorhergesagten Nichtvorkommen (Spezifität), mit durchschnittlich 37 Prozentpunkten höherer CCR und 42

Prozentpunkten höherer Spezifität. Der Prozentsatz richtig vorhergesagter Vorkommen (Sensitivität) war dagegen 18 Prozentpunkte niedriger. An 71% der Probestellen des Validierungsdatensatzes wurde die Wiederbesiedlung mindestens mit einer moderaten Modelgüte (CCR > 70%) vorhergesagt. Mit dem konservativen Modellierungsansatz wurde hingegen nur für 14% der Probestellen diese moderate Modelgüte erreicht. Für 44% der modellierten Fließgewässerinsekten zeigten die Modelle nach dem Least-Cost-Ansatz eine hohe CCR (= 100%), wohingegen der konservative Ansatz für keine der Arten eine derart hohe CCR zeigte. Modelle nach dem Least-Cost-Ansatz können daher Gewässerunterhalter unterstützen, geeignete Gewässerabschnitte für Renaturierungsmaßnahmen mit hohem Wiederbesiedlungspotenzial auszuwählen.

5.2. Schlussfolgerungen und Ausblick

Die Ergebnisse der vorliegenden Dissertation werden voraussichtlich zu einem besseren Verständnis zur Ausbreitung und Wiederbesiedlung benthischer Wirbelloser innerhalb und zwischen Gewässersystemen beitragen. In den nachfolgenden Absätzen werden die zentralen Schlussfolgerungen und methodische Einschränkungen diskutiert und Vorschläge für zukünftige Forschungsarbeiten formuliert. Da die Dissertation in zwei Hauptkapitel (Kapitel 2 und 3) unterteilt ist, erfolgt dies separat für jedes Hauptkapitel. Abschließend werden neue Erkenntnisse zur Aus- und Verbreitung benthischer Wirbelloser zusammenfassend vorgestellt, die in Studien mit Ko-Autorenschaft dieses Autors erzielt wurden.

Kapitel 2: Modellierung des Effekts aquatischer und terrestrischer Barrieren auf die Ausbreitung aquatischer Insektenarten: eine Fallstudie aus einem mitteleuropäischen Gewässereinzugsgebiet im Mittelgebirge.

Die Modellierung der Ausbreitung merolimnischer Fließgewässerinsekten ist auf verlässliche Kenntnisse zur räumlichen Lage vorhandener Quellpopulationen angewiesen aber auch zu deren Ausbreitungsfähigkeiten, bestenfalls differenziert für die verschiedenen Lebensstadien mit unterschiedlichen Ausbreitungs-fähigkeiten (larvales und adultes Stadium). Außerdem ist es erforderlich zu

wissen, ob und mit welcher Wirkung Strukturen innerhalb des Gewässers oder zwischen Gewässern Ausbreitung schwächen oder blockieren können.

Die Anzahl der Gewässerabschnitte, die von den Ausbreitungsmodellen als erreichbar prognostiziert werden, unterscheiden sich von Art zu Art. Die Modelle können bei einer räumlichen Auswertung in der Planung von Renaturierungen aufzeigen, welche Gewässerabschnitte von einer Vielzahl an Arten potenziell wiederbesiedelt werden könnten. Dies würde jedoch voraussetzen, dass Ausbreitungsmodelle für eine Vielzahl an Fließgewässerinsekten von Interesse entwickelt und angewendet werden müssten. Im Fall der Fließgewässerinsekten ist die terrestrische Ausbreitung im Flugstadium sehr viel weitreichender als die larvale Ausbreitung innerhalb der Gewässer. Deshalb wird die Ausbreitung sehr viel stärker von der Verteilung von Barrieren in der terrestrischen Landschaft (z. B. Siedlungsgebiete, dichter Nadelforst) beeinflusst als von der Anwesenheit von Barrieren innerhalb des Gewässers (z. B. Stauwehre). Die Etablierung von Populationen an einem Gewässer ist jedoch sehr viel komplexer, da hierzu nicht nur geeignete Habitate im jeweiligen Gewässerabschnitt sondern auch die Ankunft vieler Individuen einer Art benötigt werden. Die Ankunft vieler Individuen ist wiederum wahrscheinlicher für Ausbreitungsereignisse im larvalen Stadium.

Zusammenfassend unterstreichen die Ergebnisse die Bedeutung terrestrischer Ausbreitungsbarrieren für die Vorhersage von Ausbreitung. Ohne die Berücksichtigung von Barrieren zeigen die Modelle eine höhere Überschätzung der Ausbreitung als Modelle, die Barrieren berücksichtigen. Dennoch weisen die Ausbreitungsmodelle auch weiterhin Unsicherheiten auf, solange art- und lebenszyklusspezifische Ausbreitungsdistanzen weiterhin mehr auf Experteneinschätzungen und weniger auf empirischen Daten beruhen. Gleiches gilt für die Parametrisierung der Barrieren, die als Strukturen innerhalb oder außerhalb von Gewässern auf die Ausbreitung wirken. Zukünftige Studien sollten diese Wissenslücken schließen und zum Beispiel weitere Feldexperimente zu Ausbreitungsdistanzen verschiedener Arten führen oder Ausbreitungsmodelle mit populationsgenetischen Untersuchungen verknüpfen.

Kapitel 3: Anwendung und Validierung eines neuen Ansatzes zur Ausbreitungsmodellierung benthischer Wirbelloser: erste Besiedlung eines zuvor offenen Abwassersystems.

Im Vergleich zu einem allein auf Ausbreitungsdistanzen basierenden Ansatz zur Vorhersage von Ausbreitung und Wiederbesiedlung, verbesserte die Berücksichtigung von artspezifischen Ausbreitungsdistanzen und -barrieren die Vorhersagequalität von Ausbreitungsmodellen. Die richtig vorhergesagten Vorkommen und Nichtvorkommen (CCR) und zugleich die richtig vorhergesagten Nichtvorkommen (Spezifität) waren höher mit letzterem Ansatz. Die Ergebnisse der Validierung, Auch wenn die Validierung nur mäßige Modellgüten bestätigt, zeigen die Ergebnisse, dass Ausbreitungsdistanzen und -barrieren entscheidende Parameter sind, die die aktuelle räumliche Artverteilung in Gewässersystemen bestimmen. Die tatsächliche Etablierung von Populationen nach Ankunft an einem Gewässerabschnitt geht jedoch über den Rahmen dieser Studie hinaus, da dies eine Vielzahl eintreffender Individuen und eine wiederholte Probennahme über mehrere Wiederbesiedlungszyklen der jeweiligen Gewässerinsekten voraussetzen würde.

Trotz der hervorragenden Studienbedingungen im Untersuchungsgebiet mit bekannten Quellpopulationen für die Wiederbesiedlung und einer geringen Wahrscheinlichkeit für fälschlicherweise angenommene Nichtvorkommen, war es nicht möglich das aktuelle Vorkommen und Nichtvorkommen einer Art mit einer hohen Modellgüte vorherzusagen. Zukünftige Arbeiten sollten daher drei wichtige Aspekte berücksichtigen und behandeln: i) belastbare Kenntnisse zu Ausbreitungsfähigkeiten (Distanzen pro Zeiteinheit) sind erforderlich, die aus Markierungs- und Wiederfangexperimenten abgeleitet werden können; ii) Landschaftswiderstände, aufgrund von Barrieren innerhalb oder außerhalb von Gewässern, sind weiter zu ermitteln und in ihrer Wirkung auf Ausbreitungsdistanzen zu parametrisieren; iii) wiederholte Probennahmen an denselben Gewässerabschnitten und über mehrere Jahre sollten hinsichtlich der Habitateignung und der Populationsgröße der betrachteten Gewässerinsekten ausgewertet werden um so die aktuelle Wiederbesiedlung nach Ausbreitungsereignissen bewerten zu können.

Beiträge zu anderen wissenschaftlichen Arbeiten

Neben der Erstellung der vorliegenden Dissertation hat der Autor zu folgenden Studien beigetragen: Elbrecht et al. (2012), Gies et al. (2015a), Gies et al. (2015b), Schröder (2015) und Schröder et al. (2015). In der Zusammenschau, zeigen diese Studien, dass die aktuelle Verbreitung von Arten das Ergebnis einer Vielzahl von Faktoren ist und auch die Ausbreitung und Wiederbesiedlung Prozesse mit einem hohen Komplexitätsgrad sind, die nur mit stark vereinfachenden Modellen beschrieben werden können.

Elbrecht et al. (2012) analysierte genetisches Material von *Dinocras cephalotes* (Plecoptera), welches im Rahmen der vorliegenden Dissertation gesammelt. Die Ergebnisse zeigten, dass Genfluss zwischen den meisten Populationen im Ruhr-System stattfindet. Daraus kann geschlossen werden, dass Ausbreitungsdistanzen und -barrieren dieser Art mit geringer Flugfähigkeit auf lange Sicht (> Jahrzehnte) von geringer Bedeutung sind. Dennoch muss hier ergänzend angemerkt werden, dass diese Ausbreitungslimitierungen kurzfristig (< 10 Jahre) sicher insbesondere für die Vorhersage der Wiederbesiedlung renaturierter Gewässer als sehr bedeutend einzustufen sind. In Schröder (2015) hat der Autor zur Entwicklung von „Least-Cost“-Ausbreitungsmodellen für 10 benthische Wirbellose beigetragen. Diese Modelle wurden mit Habitat-Modellen verknüpft um das Wiederbesiedlungspotenzial von Gewässerabschnitten vorherzusagen. Die Ergebnisse zeigen dass beide Modellansätze, Ausbreitungsmodelle und Habitatmodelle mit Unsicherheiten behaftet sind, da die Vorhersagen stark von der Qualität der Eingangsdaten (z. B. den Annahmen zu Ausbreitungsdistanzen) abhängen.

In den Ergebnissen von Schröder et al. (2015) zeigt sich, dass das Artvorkommen und die Artenzusammensetzung in einem Fließgewässer von einem einzelnen Umweltparameter (hier: Salinität) beeinflusst werden kann. Die Studie von Gies et al. (2015a) basiert auf 225 Gewässerabschnitten, die von den Autoren beprobt wurden. In dieser Studie wurde das Artvorkommen für elf benthische Wirbellose mittels Habitatmodellen anstelle von Ausbreitungsmodellen prognostiziert und mit dem tatsächlichen Vorkommen verglichen. Die Ergebnisse zeigen, dass Validierungsansätze durch separat erhobene Datensätze zum Artvorkommen verbessert werden können, solange diese zuvor nicht in die Modellerstellung

eingeflossen sind. In Gies et al. (2015b) wurde das Artvorkommen mit Habitatmodellen vorhergesagt, die mit flächendeckend vorhandenen aber großskaligen Umweltparametern erstellt wurden. Die Ergebnisse zeigen, dass Vorhersagen zum Artvorkommen mittels großskaliger Umweltparameter nur für wenige benthische Wirbellose geeignet ist. Außerdem war die Übertragbarkeit der Habitatmodelle zwischen verschiedenen Gewässereinzugsgebieten gering, was vermutlich an unterschiedlichen Umweltbedingungen oder anhaltenden Effekten früherer Landnutzung liegen könnte.

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Appendix

Appendix to chapter 2

Table A1: Compilation of studies concerning the aquatic upstream, aquatic downstream and aerial dispersal of benthic invertebrates of benthic invertebrates, filtered exemplarily for genus Hydropsyche.

Full version of Table A1 is available on the CD-ROM enclosed to this thesis.

Appendix to chapter 3:

Table A2: Hindering (–) and facilitating (+) landscape elements for dispersal of the modelled taxa.

Table A3: Landscape elements hindering (friction costs $m^{-1} > 1$) and facilitating (friction costs $m^{-1} = 1$) dispersal of the modelled taxa.

Table A1 (excerpt): Compilation of studies concerning the aquatic upstream, aquatic downstream and aerial dispersal of benthic invertebrates, filtered exemplarily for genus Hydropsyche; full version of Table A1 is available on the enclosed CD-ROM.

ID	Citation	Journal / other	Method	ID-Art	Taxon	Order / class	Family	Genus	Dispersal stadium	Dispersal mode	Aquatic downstream	Aquatic upstream	Aerial	Dispersal barriers	Comments
39	Bagge (1995)	Entomologica Fennica	field experiment, fl	-	Hydropsyche contubernalis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial upstream flight	-	-	0-3,7 km	-	study was examined in a nea
40	Bagge (1995)	Entomologica Fennica	field experiment, fl	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial upstream flight	-	-	0-0,6 km	-	study was examined in a nea
41	Bagge (1995)	Entomologica Fennica	field experiment, fl	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial upstream flight	-	-	0-0,4 km	-	study was examined in a nea
56	Bergey & Ward (1989)	Hydrobiologia	field experiment	-	Hydropsyche spp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic downstream ar	aquatic upstream m	aquatic upstream m	-	-	-
1629	Bis & Usseglio-Polatera (2004)	http://www.eu-star.at/pdf	literature survey	-	Hydropsyche	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic passive (drift)	affinity (3 out of 5)	-	-	-	-
1630	Bis & Usseglio-Polatera (2004)	http://www.eu-star.at/pdf	literature survey	-	Hydropsyche	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic active upstrean	affinity (2 out of 5)	affinity (2 out of 5)	-	-	-
1631	Bis & Usseglio-Polatera (2004)	http://www.eu-star.at/pdf	literature survey	-	Hydropsyche	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial passive	-	-	affinity (1 out of 5)	-	-
1632	Bis & Usseglio-Polatera (2004)	http://www.eu-star.at/pdf	literature survey	-	Hydropsyche	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial active	-	-	affinity (3 out of 5)	-	-
2105	Coutant (1982)	Aquatic Insects	field experiment	-	Hydropsyche cockerelli	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial upstream flight	-	-	16 km upstream flig	-	downstream and lateral dispe
2170	Ehlert (2009)	Essener Ökologische Sc	literature survey an	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial flight	-	-	200 m in 1-3 days (	-	-
2171	Ehlert (2009)	Essener Ökologische Sc	literature survey an	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial flight	-	-	-	H. siltalai desposits the egg	-
2175	Elliott (1971a)	Oecologia	field experiment	-	Hydropsyche sp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift	living individuals sho	-	-	-	-
2195	Elliott (2003)	Freshwater Biology	field experiment	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic downstream ar	max. 1,5 m/day	max. 6,5 m/day	-	no significant difference betv	-
2232	Gellert (2011)	Proceedings of the annu	field experiment	-	Hydropsyche sp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	850 m/7 weeks	-	-	-
2233	Gellert (2011)	Proceedings of the annu	field experiment	-	Hydropsyche sp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	ca. 17 m/Tag	-	-	-
2241	Gullefors (1983)	Fauna norrlandica	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial upstream flight	-	-	compensatory flight	-	there was still a few amount c
2436	Kovats et al. (1996)	Freshwater Biology	field experiment, lig	-	Hydropsyche hageni	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	max. 5 km	-	5 km was study area extent
2437	Kovats et al. (1996)	Freshwater Biology	field experiment, lig	-	Hydropsyche phalerata	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	max. 5 km	-	5 km was study area extent
2474	Lautenschläger (2004)	PhD thesis, University of	field experiment	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift	species drifts	-	-	-	drift experiments revealed hig
2495	Malicky (1987)	Jahresberichte der Biolo	field experiment	5602	Hydropsyche saxonica	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial flight	-	-	> 3 km	-	> 3 km from source, rhithral s
2836	Poff et al. (2006)	Journal of the North Ame	literature survey an	-	Hydropsyche	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic, aerial	common occurrence	< 100 cm/h (crawlin	-	-	strong adult flying strength; n
2911	Rawer-Jost et al. (1999)	Hydrobiologia	field experiment, m	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	-	-	not constrained by fishway (	-
2912	Rawer-Jost et al. (1999)	Hydrobiologia	field experiment, m	-	Hydropsyche sp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	-	-	not constrained by fishway (	-
2972	Schmidt-Kloiber & Hering (editors	freshwaterecology.info	literature survey an	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic, aerial	-	-	-	-	high dispersal capability
2973	Schmidt-Kloiber & Hering (editors	freshwaterecology.info	literature survey an	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic, aerial	-	-	-	-	high dispersal capability
2986	Schroeder et al. (2005)	Proceedings of the annu	field experiment	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	-	-	dispersal not constrained by	-
2987	Schuhmacher (1969)	Naturwissenschaften - K	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic	-	-	-	dispersal constrained by len	dispersal constrained by lenti
2988	Schuhmacher (1969)	Naturwissenschaften - K	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic	-	-	-	dispersal not constrained by	dispersal not constrained by
2989	Schuhmacher (1969)	Naturwissenschaften - K	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic	drift is evident	-	-	-	-
2990	Schuhmacher (1969)	Naturwissenschaften - K	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic	-	120 m (from 22.10.1	-	-	validated in lab experiment
2991	Schuhmacher (1970)	International Review of H	field experiment	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift	drift, mostly behavio	-	-	-	-
2992	Schuhmacher (1970)	International Review of H	field experiment, re	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic	-	max. 120 m/6 mont	-	-	-
2993	Schuhmacher (1970)	International Review of H	field experiment, lig	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	< 2 km	-	-
2994	Schuhmacher (1970)	International Review of H	field experiment, lig	5598	Hydropsyche instabilis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	max. 300 m	aerial dispersal not constrai	-
2995	Schuhmacher (1970)	International Review of H	field experiment, lig	-	Hydropsyche ornatula	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	max. 6 km	-	-
2996	Schuhmacher (1970)	International Review of H	laboratory experim	-	Hydropsyche sp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic upstream move	-	positive rheotaxis	-	-	all larves moved upstream ove
3009	Shibata (unpublished) in Watana	Aquatic Conservation: M	observation	-	Hydropsyche orientalis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	660 m per day (esti	-	"adults fly against the wind u
3066	Umweltbundesamt (UBA) (editor)	-	literature survey	-	Hydropsyche angustipennis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	3 km	-	-
3067	Umweltbundesamt (UBA) (editor)	-	literature survey	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	8 km	-	-
3659	Vieira et al. (2006)	-	literature survey	-	Hydropsyche orris	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift propensity	strong (active / ofter	-	-	-	-
3660	Vieira et al. (2006)	-	literature survey	-	Hydropsyche orris	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic drift propensity	strong (active / ofter	-	-	-	-
3661	Vieira et al. (2006)	-	literature survey	-	Hydropsyche simulans	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift propensity	strong (active / ofter	-	-	-	-
3662	Vieira et al. (2006)	-	literature survey	-	Hydropsyche simulans	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic drift propensity	strong (active / ofter	-	-	-	-
3663	Vieira et al. (2006)	-	literature survey	-	Hydropsyche spp.	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic drift propensity	medium (mostly pas	-	-	-	-
3664	Vieira et al. (2006)	-	literature survey	-	Hydropsyche spp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift propensity	strong (active / ofter	-	-	-	-
3665	Vieira et al. (2006)	-	literature survey	-	Hydropsyche spp.	Trichoptera	Hydropsychidae	Hydropsyche	larval, adult	aquatic drift propensity	strong (active / ofter	-	-	-	-
3830	Vinikour (1981)	Hydrobiologia	field experiment	-	Hydropsyche spp.	Trichoptera	Hydropsychidae	Hydropsyche	larval	aquatic drift	> 500 m	-	-	aquatic downstream dispers	aquatic downstream dispersa
3846	Watanabe et al. (2010)	Aquatic Conservation: M	genetic study	-	Hydropsyche orientalis	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial	-	-	Cincticostella elong	-	-
3851	Wiberg-Larsen (unpublished) in S	Freshwater Biology	-	-	Hydropsyche pellucidula	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial flight	-	-	2500 m (female); 80	-	-
3852	Wiberg-Larsen (unpublished) in S	Freshwater Biology	-	-	Hydropsyche siltalai	Trichoptera	Hydropsychidae	Hydropsyche	adult	aerial flight	-	-	2500 m (female)	-	-

Table A2: Hindering (–) and facilitating (+) landscape elements for dispersal of the modelled taxa, i.e., *Anabolia nervosa* (ANAB), *Amphinemura* sp. (AMPH), *Atherix/Ibisia* sp. (ATHE), *Chelifera* sp. (CHEL), *Cordulegaster boltonii* (CORD), *Elodes minuta*-group (ELOD), *Glyphotaelius pellucidus* (GLYP), *Halesus radiatus* (HALE), *Hemerodromia* sp. (HEME), *Lithax obscurus* (LITH), *Lype reducta* (LYPE), *Micropterna lateralis/sequax* (MICL), *Micropterna nycterobia* (MICN), *Nemoura cinerea cinerea* (NEMO), *Odontocerum albicorne* (ODON), *Plectrocnemia conspersa conspersa* (PLEC), *Potamophylax nigricornis* (POTN), *Potamophylax rotundipennis* (POTR), *Potamophylax* sp. (POTS), *Sericostoma flavicorne/personatum* (SERI). The classification was based on expert and literature knowledge; recommended references are marked by footnotes.

Taxon	**Aerial**								**Aquatic upstream**					**Aquatic downstream**			
	Deciduous/mixed forest	Coniferous forest	Open land	Urban area	Road infrastructure	Culverts	Impounded water body > 1,000 m^2	water body with near natural riparian vegetation	water body with degraded riparian vegetation	water body	wastewater channel	Transverse barriers (e.g., weirs)	Culverts	Impounded water body > 1,000 m^2	water body	wastewater channel	Transverse barriers (e.g., weirs)	Culverts	Impounded water body > 1,000 m^2
CORD	-[a]	-[a]	+[a]	-	-	-	+	+	+	+	-	-	-	-	+	-	-	+	-[b, c]
LITH	+	-[d]	+	-[e, f]	-	-	-[g, h]	+[i]	+	+	-	-	-[j]	-	+	-	-	+	-[b, c]
GLYP, HALE, MICL, MICN, POTN, POTS	+	-[d]	+	-[e, f]	-	-	-[g, h]	+[i]	+	+	-	-	-[j]	-	+	-	-	+	-[b, c]
ODON, PLEC, LYPE, SERI	+	-[d]	+	-[e, f]	-	-	-[g, h]	+[i]	+	+	-	-	-[j]	-	+	-	-	+	-[b, c]
AMPH, NEMO	+[k, l]	-[d, m]	-	-[e]	-	-	+	+[i]	-	+	-	-	-	-	+	-	-	+	-[b, c]
ELOD	+	-	+	-	-	-	-	+	+	+	-	-	-	-	+	-	-	+	-[b, c]
ATHE, CHEL, HEME	-[n]	-[n]	+[n]	-	-	-	+	+	+	+	-	-	-	-	+	-	-	+	-[b, c]

[a] = Keller et al. (2012); [b] = Vinikour (1980); [c] = Vinikour (1981); [d] = Hering (1992); [e] = Smith et al. (2009); [f] = Smith & Collier (2001); [g] = Statzner (1978); [h] = Ulfstrand (1970); [i] = Ehlert (2009); [j] = Blakely et al. (2006); [k] = Macneale et al. (2005); [l] = Winterbourn et al. (2007); [m] = Briers et al. (2002); [n] = Delettre & Morvan (2000).

Table A3: Landscape elements hindering (friction costs m^{-1} > 1) and facilitating (friction costs m^{-1} = 1) dispersal of the modelled taxa, i.e., *Anabolia nervosa* (ANAB), *Amphinemura* sp. (AMPH), *Atherix/Ibisia* sp. (ATHE), *Chelifera* sp. (CHEL), *Cordulegaster boltonii* (CORD), *Elodes minuta*-group (ELOD), *Glyphotaelius pellucidus* (GLYP), *Halesus radiatus* (HALE), *Hemerodromia* sp. (HEME), *Lithax obscurus* (LITH), *Lype reducta* (LYPE), *Micropterna lateralis/sequax* (MICL), *Micropterna nycterobia* (MICN), *Nemoura cinerea cinerea* (NEMO), *Odontocerum albicorne* (ODON), *Plectrocnemia conspersa conspersa* (PLEC), *Potamophylax nigricornis* (POTN), *Potamophylax rotundipennis* (POTR), *Potamophylax* sp. (POTS), *Sericostoma flavicorne/personatum* (SERI); costs were derived from the information listed in Table A2.

Taxon	**Aerial**									**Aquatic upstream**					**Aquatic downstream**				
	Deciduous/mixed forest	Coniferous forest	Open land	Urban area	Road infrastructure	Culverts	Impounded water body > 1,000 m^2	water body with near natural riparian vegetation	water body with degraded riparian vegetation	water body	wastewater channel	Transverse barriers (e.g., weirs)	Culverts	Impounded water body > 1,000 m^2	water body	wastewater channel	Transverse barriers (e.g., weirs)	Culverts	Impounded water body > 1,000 m^2
CORD	5	10	1	10	10	10	1	1	1	1	10,000	10,000	2	2	1	5	5	1	2
LITH	1	5	1	10	10	10	5	1	1	1	10,000	10,000	2	5	1	5	5	1	5
GLYP, HALE, MICL, MICN, POTN, POTS	1	5	1	10	10	10	5	1	1	1	10,000	10,000	2	5	1	5	5	1	5
ODON, PLEC, LYPE, SERI	1	5	1	10	10	10	5	1	1	1	10,000	10,000	2	5	1	5	5	1	5
AMPH, NEMO	1	10	5	10	10	10	1	1	5	1	10,000	10,000	2	5	1	5	5	1	5
ELOD	1	5	1	10	10	10	5	1	1	1	10,000	10,000	2	5	1	5	5	1	5
ATHE, CHEL, HEME	5	10	1	10	10	10	1	1	1	1	10,000	10,000	2	2	1	5	5	1	2

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